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IDENTIFICATION OF PHYSIOLOGIC RACES OF PUCCINIA GRAMINIS VAR. TRITICI

General Concepts

Wheat stem rust, *Puccinia graminis* var. *tritici*, comprises an indefinite number of biotypes which differ in pathogenicity and other physiologic characters. The present publication, like its predecessors of 1922 and 1944, is intended as a guide to the identification and classification of biotypes

or groups of biotypes into physiologic races.

The term "biotype" connotes a population of individuals of the same genotype, that is, with the same genetic constitution. Theoretically, the progeny of a single normally dicaryotic aeciospore or urediospore should constitute a biotype, but mutation may convert an originally homogeneous population into a heterogeneous one. Moreover, the original spore from which a monosporic line was derived may have contained more than two nuclei; consequently, dissociation or possibly some form of parasexualism may result in the production of new biotypes and thus destroy the genetic purity of the line. In any case it would be impossible to prove that different isolates belong to the same biotype, because they would have to be identical in all characters, and there is no certainty that all characters are even known. The term "biotype" is therefore used only in a conceptual sense in this paper.

Physiologic race is the only taxon—taxonomic category—that is recognized within var. *tritici* in this publication. Physiologic race can be defined as "a biotype or group of biotypes, within a species or lower taxon, which can be distinguished with reasonable facility and certainty from other biotypes or groups of biotypes by physiologic characters, including pathogenicity." This definition requires only that the differences be physiologic; it neither requires nor excludes differences in pathogenicity. Nor does it imply that physiologic races differ exclusively in physiologic characters, but stipulates only that such characters be the basis for classification. The "reasonable facility and certainty" is a general require-

ment for any useful system of classification.

It is becoming increasingly evident that *P. graminis* var. *tritici* comprises an indefinite number of biotypes, as is true also of wheat, barley, rye, and several hundred wild grasses which are subject to its attack. If it were possible to inoculate, under the same environmental conditions, all biotypes of wheat, barley, rye, and wild grasses with all biotypes of var. *tritici*, virulence probably could be represented by a regression line with very small intervals between the points representing the virulence of each of thousands of biotypes. The composition of this vast population of biotypes is changing continually, both in respect of the kinds and the relative numbers of each kind. In North America, and in other areas, some rust races have appeared and disappeared; others, notably races 1 and 11, have appeared, disappeared and reappeared. But how nearly identical the genotypes of these races were before and after the period of absence is not known, even though the infection types on the standard differentials often agreed perfectly.

Because of changing and shifting populations of the innumerable biotypes of the rust and the continual production of new combinations of genes in new varieties of wheat, it would be difficult to devise a perfect system for classifying rust races for all scientific and practical purposes at any given time. Therefore, a system is desirable which combines continuity with flexibility—historical perspective with new knowledge regarding races. There is interest and value in knowing that some races have come and gone and then returned again; and there is value in knowing that certain isolates appear essentially alike on the 12 standard differentials but are clearly different on certain other varieties.

The ultimate aim in classification of rust races is a system based on adequate knowledge of genetic relationships. Until the necessary information is obtained, however, it is important to continue using a uniform set of standard differential varieties for grouping biotypes that have a number of distinctive characters in common and can therefore be designated as races.

Collection and Preservation of Rust Samples

Collection of rust samples. The objectives of race identifications determine what should be collected, and common sense determines how collections should be made. Obviously, the aim should be to obtain an adequate sample for the purposes of the study. As purposes and scope may vary, however, the criteria for adequate sampling must be determined in individual cases.

When the principal objective is to determine the identity and prevalence of all races in an area, collections should be made in all ecological zones and from all kinds and varieties of host plants in each zone. Sometimes it is especially important to collect from wild grasses, because some of them are susceptible to more races than are the prevalent varieties of wheat, as is conspicuously true of *Hordeum jubatum* L. in certain areas of North America.

Knowledge regarding the reaction of wheat varieties to different rust races is an aid to discriminating sampling in commercial fields and rust nurseries. A prime practical objective in all surveys should be the early detection of new or dangerous races, and the intelligent use of indicator varieties can be useful in attaining the objective.

The relatively standardized procedures for identifying rust races in glasshouses or other types of plant houses should be supplemented by experimentation and observation in the field. In addition to regular breeding nurseries, special-purpose nurseries containing indicator and test varieties of wheat and other susceptible crops should be maintained, as an aid in determining the presence and prevalence of the various races and their effects on adult plants under the prevailing environmental conditions. Such nurseries should contain all standard and supplemental differential varieties and any others whose rust reactions it is important to know. National and international nurseries should be utilized wherever feasible.

As it is desirable to know the relative amounts of all races present on important and potentially important varieties in the field, samples for identification should be selected as discriminatingly as possible. At least one sample, preferably several, should be taken from each variety. There sometimes is a tendency to collect a disproportionate number of samples from the most heavily infected varieties, which is the easiest but not the best procedure, because samples from varieties with light infection may contain races with special and important pathogenic characters. In taking the rust samples, it is important to avoid contaminating the hands with spores; otherwise each successive sample may contain some spores from all preceding samples. Glassine end-opening envelopes, about 9 cm. by 17.5 cm., are useful for collecting and containing the samples. When plants are fairly heavily and uniformly rusted, the tops of culms can be cut off just above the desired portion, which can then be inserted part way into the envelope and held from the outside while being cut to lengths which permit folding the open end of the envelope.

Preservation of inoculum. It is usually necessary to preserve rust collections for a short time, and it is sometimes desirable to preserve "rust stocks" for a long time. Spores survive best when kept cool and fairly dry; heat and high humidity are deleterious. Ordinary precautions usually suffice to preserve the viability of spores in transit from the field to the greenhouse, but special facilities are needed when collections are stored for a considerable time in order to systematize race identification or to await favorable weather. Uredial collections can be preserved for several months or even a year in a refrigerator kept at a temperature of about 40°F, and relative humidity of 40 to 50 percent.

For long-time storage of "stock cultures" or "living herbaria," a modification of the Sharp and Smith vacuum method, as described by Stewart, is useful (6, 11). The apparatus used is shown in figure 2. Fresh urediospores are placed in a pyrex glass vial about 8 mm. in diameter and 120 mm. in length. The sample is then air dried at room temperature (50-95°F.) for 48 hours or longer, after which an equal volume of recrystallized hemin is placed in the vial and mixed thoroughly with the

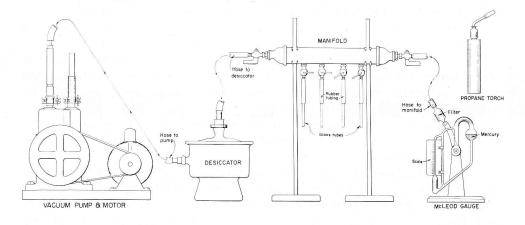


Figure 2.—Apparatus for drying urediospores in vacuum prior to long-time storage.

spores⁴. The spore-mixture is then dried for 2 hours in a vacuum system equivalent to about 1 mm. pressure reading of mercury on a McLeod Gauge. The vial is then sealed by heat from a propane torch and, after cooling for a few minutes, is placed in a refrigerator kept at 40°F. Spores stored in this way have retained their viability for well over 5 years.

Loegering et al. have found recently that urediospores can be frozen in liquid nitrogen (-195°C.) and will germinate normally if thawed at 40°C., thus suggesting another possible method for long-time preservation (1).

Inoculation Techniques

Growing plants for inoculation. Plants for inoculation can be grown in any suitable container, 4-inch clay pots being one of the most common. It is well to disinfect the soil and the seed to reduce danger of root rots. If containers are used repeatedly, they should be disinfected occasionally with live steam. Plants should be well spaced in the pots, about 15 per 4-inch pot. They should be grown in good soil, under good light, at a temperature of 68-75°F., and in a rust-free room. They can be inoculated when 2 to 4 inches tall.

Methods of inoculation. If field collections contain too little rust for inoculating all differential hosts immediately, the generally susceptible variety Little Club (or Jenkin) is inoculated in order to increase the amount. A solution of "Trimtone" (48.3 percent maleic hydrazide, sodium salt), 0.4 gram per liter of water, is sometimes added at the rate of 50 cc. to each 4-inch pot when the plants to be inoculated are 0.5 to 1.0 inch tall, as it tends to increase and prolong sporulation. This treatment dwarfs the plants somewhat and therefore eliminates the need for removing secondary leaves of the rusted plants which are used for inoculating by the dusting-brushing method. As the total effect of Trimtone is not yet known, however, it is not added regularly to the standard differentials. Moreover, it persists for some time in clay pots to which it has been added and therefore it is best not to use them for the standard differentials, at least until the chemical has been removed by soaking the pots in hot water.

When there is enough rust in a collection, all differentials are inoculated at the same time.

For all methods of surface inoculation, it is advantageous to rub plants gently between moistened fingers, then atomize them with distilled water, apply the inoculum, and immediately atomize again in order to produce initial "dew" on the plants.

Inoculum usually is applied in one of three ways⁵: 1, by means of a spatula; 2, by dusting or gently brushing with rusted plants; 3, by means of a "baby cyclone."

The *spatula* method is useful when initial inoculum is scarce in a collection or when inoculations are made with spores from individual pustules of different types in mixed infections. A satisfactory spatula can be made by flattening the end of a dentist's explorer tool. In making inoculations, spores are taken from rusted material with a wet spatula and applied to plants by running the spatula gently over the surface in such a way as to

ensure uniform distribution of inoculum. The inoculated plants are put immediately into an incubation chamber.

The *dusting* method is convenient for inoculating large numbers of plants when inoculum is abundant. The plants to be inoculated are atomized in an incubation chamber. The rusted material is held close to them and shaken gently to provide a uniform shower of spores, then brushed gently over the plants several times to ensure adequate and uniform inoculation. After this, the plants are again atomized and the incubation chamber is closed. This method is economical of labor and provides for random distribution of spores, which is important when there are two or more races in collections to be identified. There is little danger of contamination if ordinary precautions are taken.

The *cyclone* method is useful for collecting spores and making inoculations, as described by Tervet and Cassell (12). Several modifications of their cyclone have been made, one of which, the "baby cyclone" developed by Goto and Stewart in 1952, is described in figure 3. A spore-talc mixture is placed in the glass or metal vial and is then dusted on the differential varieties. By reversing the valve in the rubber bulb, spores can be collected in the vial by suction. Spores collected from a few pustules in this way often are sufficient to inoculate a complete set of the standard differentials.

General suggestions for inoculating. Whatever the method of surface inoculation, the objective should be to distribute a moderate number of viable spores uniformly on the moistened surfaces of the plants. Spores that are shaken or scooped gently from uredia or aecia usually germinate better than those that are scraped off forcibly, probably because there is a tendency to scrape too deep and thus remove immature spores. Very dry uredial and aecial material should be kept in a moist chamber for several hours immediately prior to using it as inoculum. Good aecial inoculum can sometimes be obtained by placing aecial material above a glass slide in a small moist chamber until the spores have been discharged naturally.

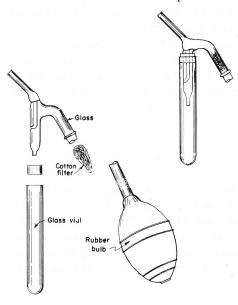
The aim in inoculating differential varieties should be to produce an adequate sample of infection types sufficiently separated to permit clear observation and the making of isolations from pustules of each type if necessary. Special care is advisable when initial inoculations are made with

⁴ Hemin has prolonged the viability of spores in experiments made at the Cooperative Rust Laboratory at Minnesota, but some investigators have reported that it had no value in their experiments.

⁵ The injection of a suspension of spores into plants by means of a hypodermic syringe has long been practiced for special purposes, especially for inoculating plants in susceptible border rows in rust nurseries. The method is also useful in establishing cultures in the greenhouse, especially when inoculum is scarce or when the viability of spores is low, as is likely to be true of old collections and of aecial material. An additional advantage is that the inoculated plants need not be kept in a moist chamber, which is necessary when they are inoculated superficially. The method is not suitable, of course, for inoculating differential varieties in race determinations because the characteristic infection types do not develop.

field collections, which may comprise several races that can be identified only by making inoculations with isolates from pustules of various types.

Noninoculated check plants should be placed in strategic positions and



collecting spores and making inoculations. (Metal may be substituted for glass.)

then treated subsequently in the same way as inoculated plants. If appreciable rust develops on the checks, it is essential to ascertain the reason and to modify procedures accordingly.

Incubation

Inoculated plants should be put immediately into an appropriate incubation chamber, unless they are already there, as in the dusting and cyclone methods. The aim in incubation is to induce and maintain "dew" on the plants for about 12 hours.

Many kinds of incubation chambers are in use. The ideal is "built-in chambers," arranged in series, equipped with devices to create artificial fog within each chamber, and located in Figure 3.—Diagram of baby cyclone for a temperature-controlled incubator room. Most chambers, however, are much simpler and less expensive.

A simple chamber consists of three parts: (1) a galvanized-iron pan, 24 × 24 inches square and 2 inches deep, into which about 1/2 inch of water is placed; (2) an open-end square made of the same material, 22 × 22 inches and 12 inches high, which should fit into the pan easily; and (3) a removable cover of plexiglass or similar non-breakable material. The cover should fit closely enough to maintain high humidity within the chamber and thus promote the development of a fine film of moisture on the plants. An incubation chamber of the above dimensions will hold twenty 4-inch pots and thus accommodate a complete set of standard differentials and several additional test varieties (Fig. 4).

The length of time required for incubation varies with conditions, although the long periods previously recommended are not necessary if favorable conditions can be provided. Under conditions favorable for "dew" formation, 12 hours are ample and 8 often suffice. Fair infection has sometimes been obtained when plants were incubated 6 hours, and occasional pustules have appeared when the period was 4 hours. It is recommended, however, that about 12 hours be adopted. A good practice is to inoculate in the late afternoon, try to provide for reduced temperature at night, and remove the pots during the cool of the next morning, so that the plants will dry slowly, and then distribute the pots to their designated places. A temperature of 70-75°F, and at least 1000 footcandles of light are desirable after removal from the incubating chamber.

The Standard Differential Varieties

The 12 "standard differential varieties" were selected as representatives of several hundred that were tested for the purpose, beginning in 1916, when the first conclusive evidence was obtained for the existence of races within the "biologic form" tritici. The varieties tested included representatives of Triticum compactum Host, T. vulgare Vill. (=T. aestivum L.), T. spelta L., T. durum Desf., T. dicoccum Schrank, T. monococcum L., T. polonicum L. and T. turgidum L. Twenty-five varieties were regularly used as differentials for about two years, during which some of them always behaved alike. As an example, Marquis, Haynes Bluestem, Glyndon Fife, and several other hard red spring wheats had consistently reacted alike, and Marquis was selected as the representative of the group. Similarly, one representative of each of several other groups was chosen, thus reducing the number of differentials from 25 to 12.

The question as to the adequacy of the differential varieties arose as soon as it became evident that there were many rust races. As new varieties of wheat were produced, therefore, they also were tested as potential differentials; and in some cases systematic search was made for varieties that would distinguish clearly between isolates that seemed to be slightly different on the standard differentials. The failure to find additional differentials for a number of years probably is partly due to the fact that the pioneer breeding for rust resistance in North America was based on relatively few resistant varieties. As the base was broadened, however, some of

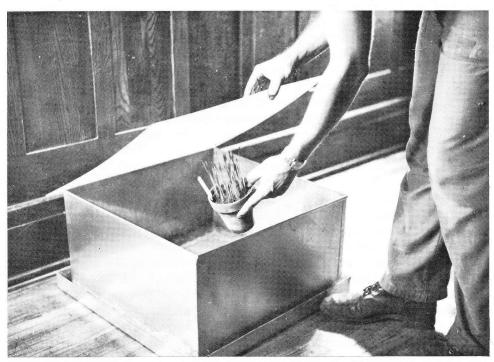


Figure 4.—A simple incubator consisting of a galvanized-iron pan and square frame to support removable top. (For further details, see page 10.)

the new varieties proved useful and are now used as supplemental differentials.

There are sound reasons for continuing to use the standard differentials. Although they do not reveal all that needs to be known about the indefinite numbers of biotypes of the *tritici* variety of *P. graminis*, they are representatives of *Triticum compactum*, *T. vulgare*, *T. durum*, *T monococcum*, and *T. dicoccum* and enable a grouping of rust biotypes which is roughly analogous to the grouping of wheats themselves into the larger categories. This first grouping of rust races may be sufficient for some purposes but it is sometimes essential to use additional differentials also, as the variety Lee is regularly used to distinguish between races 15 and 15B. In any case, the standard differentials constitute the only link with the past and are therefore useful in maintaining perspective on population trends of races.

Identification of Races by Means of the Standard Differentials

The essential information for the identification of races is given in tables 1 to 4.

Infection types and use of key. The standard differentials are listed in table 1. Purity of seed stocks is essential. Although there is relatively little cross pollination in wheat, it is well to separate increase plots of the different differential varieties in the field in such a way as to minimize the likelihood of natural crossing. Precautions should also be taken to avoid

mechanical mixing of seed.

The infection types (Table 2 and Fig. 8) can be considered as characters resulting from the growth of certain rust races on certain living substrates, the differential varieties of wheat, under certain environmental conditions. The characters are distinctive for each race-variety combination within a certain range of environmental conditions, but the range differs for different combinations and must therefore be determined for each one. As environmental factors can affect the rust race, the differential variety, and the interaction between the two living systems, they can cause considerable phenotypic variability in infection types. This variability is relatively unimportant in race identification if it does not transcend the limits of the infection types, but it is very important if it transcends the reaction classes on which the key is based (Table 2).

Temperature and light have an especially strong effect on the vari-

ability of infection types, particularly types 2 and X.

So strong is the effect of temperature on some race-variety combinations that different races could be identified as the same race at a given temperature and the same race could be identified as two races at different temperatures. Thus, races 49 and 139 are distinct at temperatures below 75°F., as race 49 produces infection type 4 and race 139 produces type 2 on Marquis and Kota, the two essential differentials for these races, indicating that both varieties are susceptible to 49 and resistant to 139. At higher temperatures, however, both varieties are susceptible to both races, as race 49 continues to produce type 4, and race 139 also produces type 4 instead of type 2; hence race 139 looks like 49 and the two races

cannot be distinguished with certainty, as the difference in infection types on Reliance, 0 for 49 and 1 for 139, is not always distinctive.

The difficulties in identification due to the variability of infection types 2 and X in some race-variety combinations is illustrated by three pairs of races: (A) 17 and 29; (B) 38 and 39; (C) 11 and 32. The infection types given for these races in table 4, with plus and minus signs omitted except for Khapli, are given below.

	LC	MA	REL	KO	ARN	MND	SPM	KUB	AC	ENK	VER	KPL
(A) 17	4	4	0;	3	4	4	4	3	3	3	1	1 =
29	4	4	0	3	X	X	X	X	X	3	1	1-
(B) 38	4	2	4	3	X	X	X	X	X	4	1	1+
39	4	2	4	3	4	3	4	4	3	4	1	1-
(C) 11	4	4	3	3	4	4	4	3	3	3	1	1 =
32	4	4	4	3	X	X	X	X	X	3	1	1-

The two races of group A are always distinct from those of groups B and C because of the nonvariable 0 on Reliance, but 17 and 29 are not always distinguishable from each other because 29 can produce types 3 and 4 instead of X on the durums at high temperature and therefore may look like race 17.

The intergroup difference between B and C is on Marquis, with infection types 2 and 4, respectively; and the intragroup differences are that one race of each pair produces types 3 and 4 on the 5 durums, Arnautka—Acme, and the other produces type X. But those race-variety combinations that produce types 2 and X at moderate temperature can produce types 3 or 4 at high temperature and under certain light conditions; therefore both the intergroup and the intragroup differences may not be apparent under such conditions. Accordingly, types 3 or 4 can be substituted, independently or jointly, for types 2 and X in the table of infection types in order to show the possible phenotypes. As types 3 and 4 both indicate susceptibility, type 4 alone is used in indicating the results of the substitution. The replacement of type 2 by type 4 indicates a change in reaction class from resistant to susceptible, and the replacement of type X by type 4 indicates a change from mesothetic to susceptible; hence the races that are characterized by type 2 or type X, or both, may look like certain other races at high temperature and appropriate light. This is indicated below by the equals sign, which means only that the races on the left may have phenotypes, under special conditions, similar to the common phenotypes of the races on the right.

```
Race 29 — Substituting type 4 for type X = race 17

Race 38 — Substituting type 4 for type 2 = race 32

— Substituting type 4 for type X = race 39

— Substituting type 4 for types 2 and X = race 11

Race 39 — Substituting type 4 for type 2 = race 11

Race 32 — Substituting type 4 for type X = race 11
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The variable races are 29, 38, 39, and 32; the constant ones are 17 and 11. A variable race may look like one or more of the constant races, but the reverse is seldom true. Thus, the facts are as follows, assuming high temperature and appropriate light:

Race 29 may look like race 17 Race 38 may look like races 32, 39, or 11 Race 39 may look like race 11 Race 32 may look like race 11

It is evident, therefore, that a culture which appears to be race 11 during a period of hot weather may actually be race 11, race 38, race 39, race 32, or a mixture of any or all of the four. How can the races in such a mixture be detected and identified? The best procedure, of course, is to test the culture at a temperature of about 70°F. if possible; if not, clues can sometimes be obtained from minor differences in infection types. If some of the apparently type-4 pustules on Marquis are surrounded by a faint chlorotic halo, an experienced observer will suspect that they may be caused by one or more races, such as 38 and 39, which produce type 2 at lower temperature. Indeed, some races which normally produce type 2 on Marquis produce a "pseudo 4" but not a "true 4" at high temperature. Although the infected area and the pustules may be as large as those of a true 4, a faint chlorotic-necrotic band is perceptible around the pustule, especially with transmitted light. In such cases isolates should be obtained from the pseudo type-4 and true type-4 pustules for comparative study. Similarly, there sometimes are slight indications of a potential type X on the durums. Race 38 sometimes betrays its presence in a mixture such as that under consideration by infection types on Kota and Khapli. The mean infection types recorded in table 4 for race 38 on Kota and Khapli are 3- and 1+, respectively, whereas the corresponding types for races 11, 32, and 39 are 3+ and 1- or 1=. Hence the presence of small type-3 pustules among larger ones on Kota and of large type-1 lesions among smaller ones on Khapli indicates the possible presence of race 38. Comparative studies of isolates obtained from the different kinds of pustules on Kota and Khapli often prove the presence of race 38 and one or more of the other races.

Obviously, it is important to learn which race-variety interactions, as represented by the infection types, are thermolabile and which are thermostable.

As types 2 and X are very variable in some race-variety combinations, race identifications should be made under environmental conditions which permit the most characteristic infection types to develop. The alternative is to find supplemental differentials which function satisfactorily under all environmental conditions. In the present state of knowledge the principal reliance must still be on controlled conditions.

Although the precise effects of light are not so well known as those of temperature, light can affect the infection type considerably. It has been emphasized repeatedly that a temperature of about 70°F. and sufficient

light, preferably more than 1000 foot-candles, are most conducive to the development of distinctive infection types. Some races cannot be identified with certainty when temperature and light deviate too far from the optimum. If favorable conditions cannot be provided, therefore, it should be recognized that the identifications are tentative only.

Assuming favorable conditions for rust development and the presence of single races in collections, the identification of races is simple, as the trichotomous key (Table 3) is based on only three reaction classes: resistant, mesothetic, and susceptible, as described in table 2. Table 4, a record of the mean infection types produced by 294 races, is an essential supplement to the key, which utilizes the reactions of only a few differentials for some races. Thus, only seven of the differential varieties are used for the preliminary identification of race 130 and race 236. If the key indicates race 130 and the infection types produced on the other five differentials agree with those given in table 4, the culture is race 130 according to the criteria in the key and the table. The key requirements for race 130 are that Little Club, Marquis, Kota be resistant and four durums susceptible. The complete description, however, requires that the additional Acme durum and Einkorn be susceptible also, and that Reliance, Vernal emmer, and Khapli be resistant. If the reaction class of any of these five differential varieties is different from that given, the culture represents a new race, unless a mistake has been made. If one or more infection types deviate clearly and consistently but remain within the reaction class, however, the requirements for race 130 are still satisfied, but the culture is different from those on which the description was based. Assuming that the unknown culture consistently produced type 2 on Reliance instead of 0 as in the table, the infection type is different from that produced by the "type specimen," but the reaction class remains the same. And yet the "unknown" is different and should not be ignored; it deserves a designation if the character in which it differs is distinct and consistent enough to justify the conclusion that the difference is genetic and not merely phenotypic. Races 59 and 15 are good examples.

The infection types produced by race 59 and by 59A, 59B, and 59C are essentially alike on all of the differentials except Reliance and Kota, on which they differ as shown below.

	Reliance	Kota
59	0	0;
59A	2	0;
59B	2	2
59C	0	2

For several years after race 59 was first encountered, all isolates produced 0 and necrotic flecks on Reliance and Kota, respectively. Subsequently, however, isolates that differed from the "type" were obtained from barberry-infested areas in the chronological order represented by the letters. Although the infection types differ clearly and consistently on Reliance and Kota, both are resistant to the four kinds of isolates, which therefore conform to the criteria for race 59 in the key. Nevertheless, the difference between types 0 and 2 is so distinct and consistent as to indicate that the

four kinds of isolates are genetically different, and they are therefore designated differently, as indicated above.

Race 15 also illustrates the fact that different isolates of a given race may produce different infection types within reaction classes of the standard differential varieties of wheat. Shortly after race 15 was first found in 1918, there were indications that isolates differed somewhat in virulence, but attempts to find ways of conclusively demonstrating the differences were unsuccessful. Subsequently, however, an isolate from Japan was distinct enough to justify special designation, as 15A, because of its perceptibly lower virulence on the standard differentials (2). Later, a Brazilian isolate that was exceptionally virulent on the standard differentials was designated as 15B. Still later, it was found that there were differences among the group of isolates designated as 15B.

The differences in infection types within reaction classes on the standard differential varieties, such as those described above, indicate that there are genetic differences among isolates of some rust races. Most races probably comprise a number of different biotypes which may or may not be distinguishable on the standard differentials. Even if they are distinguishable, however, their importance can be determined only by inoculating additional varieties; accordingly, they are discussed further in the section on supplemental differentials.

The identification of races in mixtures. Field collections often contain a mixture of races. Sometimes it is possible to identify the races in the mixture because only certain combinations of races could cause the particular combination of infection types. For example, race 17 produces type 3 or 4 and 19 produces type 2– on Marquis, but they are essentially alike on the other 11 differentials. As 17 and 19 are the only known races that produce this combination of infection types, their presence and the percentage of each in a mixture of the two can be determined directly. Direct identification is not always possible, however, and it is then necessary to make isolations from pustules of the various types, as illustrated in figure 5.

Mixtures usually are most apparent on Marquis, Arnautka, Mindum, Spelmar, Einkorn, and Vernal. On Marquis there often are type-2 and type-4 pustules. On the three durums and on Einkorn and Vernal there often are two sharply distinct types, type 1 and type 3+ or 4. Mixtures on Marquis are not always clear, however, because heavy infection of type 4 may tend to obscure that of type 2. Moreover, at high temperature certain races that normally produce type 2 may produce a type resembling 3 or 4=. Mixtures may sometimes resemble type X, but the intergrading of pustule types that is so characteristic of type X is seldom present in mixtures.

It is important to inoculate with a random sample of the rust in collections. Random distribution of inoculum is best attained by the dusting-brushing method or by the cyclone method described under Inoculation Techniques. It often is possible to determine the percentage prevalence

⁶ This section is copied from Stakman, Levine, and Loegering (9), with slight changes only.

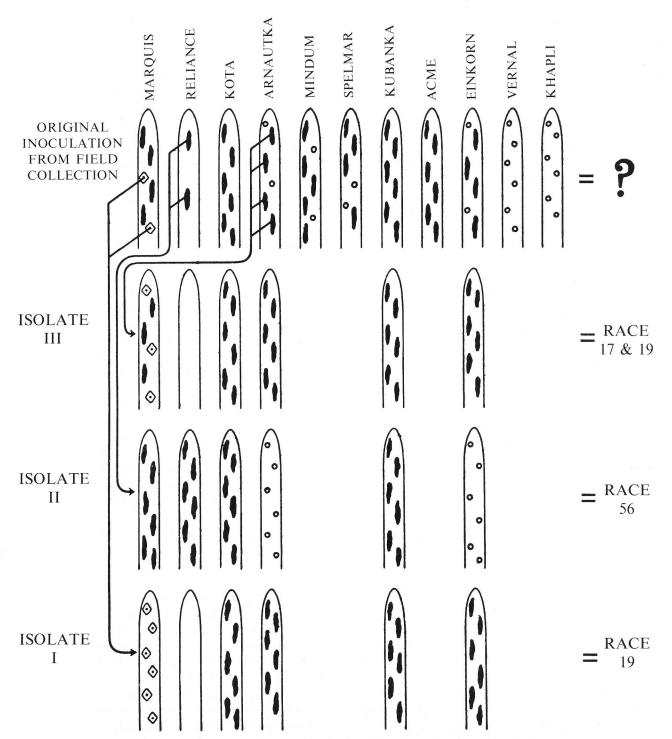


Figure 5.—Diagram showing method of isolating races from a mixed field collection. Circles indicate type-1 infection; diamonds indicate type 2; solid black spots indicate types 3 and 4.

of each race in a mixture by visual inspection. As an example, mixtures of races 17 and 56 would produce the following infection types:

It can be concluded that races 17 and 56 are present if the number of pustules on Reliance corresponds with the number of flecks or type-1 pustules on Arnautka, Mindum, Spelmar, and Einkorn, and if the number of type-3 or type-4 pustules on Arnautka, Mindum, and Spelmar corresponds with the number of similar pustules on Einkorn. It is then possible also to estimate the relative proportions of the two races in the collection.

Figure 5 represents the results of inoculating the differential varieties of wheat with rust as it was obtained from the field. There are two infection types, 4 and 2, on Marquis; hence there are at least two races in the eulture. On Reliance there are type-4 pustules only, but the number is only about 33 percent of the total number of pustules on Marquis. On Arnautka, Mindum, Spelmar, and Einkorn the number of type-1 pustules corresponds with the total number of pustules on Reliance. It seems likely, therefore, that the race causing the large pustules on Reliance is causing the small ones on the three durums and Einkorn. It might also be producing the type-2 pustules on Marquis, but knowledge of races makes this seem doubtful. The most likely combination would be races 17, 19 and 56, but this is not certain. Therefore the inoculations indicated in figure 5 were made, and the results prove that the surmise was correct. In this case, then, three isolations were made: Isolate I proved to be pure race 19; isolate II was pure race 56; and isolate III contained races 19 and 17, the only distinctive difference between them being that 17 produces type-4 pustules on Marquis and 19 produces type 2. Pure race 17 could have been obtained. if necessary, by making an isolation from type-4 pustules on Marquis in isolate III.

The three isolates obtained from this collection of rust represent three "race isolates" and in the records the number of race isolates corresponds both with the number of isolations made and the number of races identified. The ratio of collections to isolates is 1:3 in this case, as three race isolates were obtained from a single collection. This would still have been true if four actual isolations had been necessary to demonstrate the presence of the three races. In the illustration chosen, several other methods could have been used for arriving at the same result. A limited number of the differential varieties, known as a "half series," could have been inoculated with rust from the type-1 pustules on the three durums or Einkorn (after increasing the rust on a susceptible variety to obtain enough inoculum), but race 56 would have been identified from these isolations as it was when transfers were made from Reliance. Even though race 56 had been obtained in several series of isolations from one collection, however, it still would count as one race isolate. In the records, then, "race isolates," or simply "isolates," does not refer to the number of operations required to identify

races but to the number of times each race was identified in all of the collections processed.

A "half series" is shown in figure 5 and includes the varieties Marquis, Reliance, Kota, Arnautka, Kubanka, and Einkorn. Arnautka, Mindum, and Spelmar react alike to many of the common races of stem rust, as do Kubanka and Acme. Therefore, after observing similar mixtures of type-4 and type-1 pustules on Arnautka, Mindum, and Spelmar, and complete susceptibility on Kubanka and Acme, it is sufficient to inoculate one variety from each group. Arnautka and Kubanka are commonly used for this purpose. As Vernal and Khapli were resistant in the illustrations used, it must be concluded that they are resistant to all races in the mixture and need not be tested further; however, if there are two or more infection types on either variety, it must be included in the "half series." If there is doubt concerning an identification made on the basis of a "half series," the isolate is tested on the complete set of differentials.

Some supplemental differential varieties, such as Bowie, are useful in detecting races whose presence may be masked by others in mixtures. Thus, 15B may mask the presence of a low percentage of races 11E, 29, or 48A, especially at high temperature. Assuming that 95 percent of the rust in a mixture of these four races is 15B, Lee and all standard differentials except Khapli would have type-4 pustules, which would tend to obscure the lower infection types produced by the other races on varieties resistant to them. The presence of large pustules on Bowie, however, would immediately indicate the presence and the approximate percentage of one or more of the three races mentioned above. In some cases the presence of large pustules on Bowie merely confirms the probabilities indicated by the infection types on the standard differentials and Lee. In other cases there are alternative possibilities, but Bowie has been susceptible to only a few North American races up to the present time; therefore, it has been very useful in detecting their presence in mixtures and in identifying them by inoculating the differential varieties with isolates from large pustules which appear on it.

Original Collection and Identification of Races 1-297

Data are given in table 5 regarding the original collection and identification of the 297 races listed. The race numbers were assigned by the Minnesota Cooperative Rust Laboratory on the basis of original or confirmatory studies of the isolates themselves or on the basis of the infection types recorded and furnished to the Laboratory by the identifier. In the latter case the infection types for the isolates in question were compared with those previously recorded for published and for unpublished races, and a new race number was assigned if the evidence justified it. In some doubtful cases it was suggested that additional studies be made of individual isolates or that recognition of an apparently new race be deferred until more isolates of the same kind were found. In general, however, the competence of the investigators justified complete confidence in their data. This cooperative effort has made possible an approach to an international register of races of wheat stem rust.

Table 1.— Standard differential varieties of *Triticum spp.* used in identifying physiologic races of *Puccinia graminis* var. *tritici*.

Triticum compactum
Little Club, C.I.^a 4066^b

Triticum vulgare
Marquis, C.I. 3641
Reliance, C.I. 7370^b
Kota, C.I. 5878

Triticum monococcum Einkorn, C.I. 2433 Triticum durum

Arnautka, C.I. 1493 Mindum, C.I. 5296 Spelmar, C.I. 6236 Kubanka, C.I. 2094 Acme, C.I. 5284

Triticum dicoccum

Vernal, C.I. 3686 Khapli, C.I. 4013

a C.I. = Cereal Investigations accession number, U.S. Department of Agriculture.

b Certain lines of Jenkin, C.I. 5177, notably Hood, C.I. 11456, may be substituted for Little Club; and generally, Kanred, C.I. 5146, for Reliance.

Table 2.—Infection types produced by physiologic races of *Puccinia graminis* var. tritici on standard differential varieties of *Triticum spp.*, corresponding varietal reactions, and varietal reaction classes used in key for identifying races (Table 3).

Infection type ^a	Varietal reactions and reaction classes b
	Resistant
O	IMMUNE—No uredia nor other indications of infection
0;	NEARLY IMMUNE—No uredia, but hypersensitive flecks present
1	VERY RESISTANT—Uredia minute; surrounded by distinct necrotic areas
2	MODERATELY RESISTANT—Uredia small to medium; usually in green islands surrounded by a decidedly chlorotic or necrotic border
	Susceptible
3	MODERATELY SUSCEPTIBLE—Uredia medium in size; coalescence infrequent; no necrosis, but chlorotic areas may be present, especially under unfavorable growing conditions
4	VERY SUSCEPTIBLE—Uredia large, and often coalescing; no necrosis, but chlorosis may be present under unfavorable growing conditions
	Mesothetic
X	HETEROGENEOUS—Uredia variable, sometimes including all infection types and intergradations between them on the same leaf; no mechanical separation possible; on reinoculation small uredia may produce large ones, and vice versa

^a Plus and minus signs are used to indicate variation within a given infection type: ++ and = indicate the upper and lower limits, respectively, of each type. The symbol \pm indicates a variation between + and - for the type. The symbol ϵ indicates exceptionally pronounced chlorosis; ϵ indicates browning with a tendency toward necrosis; ϵ indicates a tendency toward necrosis.

 $^{^{}b}$ These classes were established primarily to facilitate identification of rust races rather than to indicate degrees of resistance of wheat varieties. Thus, infection type 2 is considered to indicate resistance and type 3 to indicate susceptibility, although a variety with infection type 2++ may appear more susceptible for practical purposes than one with type 3=. Moreover, the mesothetic class is based solely on the presence of infection type X, and there can be a wide range of susceptibility and resistance within the class, as indicated by the plus and minus signs after the X.

Table 3.—Key for identifying physiologic races of *Puccinia graminis* var. *tritici* on the basis of the reactions of 12 standard differential varieties of *Triticum spp*. ^a

	Physiologic Race (key	Races with some similarities
Reaction of Differential Varieties	number)	to those at left of vertical line
Little Club resistant		
Marquis resistant		
Kota resistant		-
Arnautka resistant		
Mindum resistant		* .
Spelmar resistant		
Kubanka resistant		
Vernal resistant		103, 138
Vernal mesothetic		103, 294
Kubanka susceptible	239	
Spelmar susceptible	243	
Mindum susceptible	234	
Arnautka susceptible		
Mindum resistant	235	The state of the s
Mindum susceptible		9
Spelmar resistant	240	
Spelmar susceptible		
Kubanka resistant	236	
Kubanka susceptible		
Kota susceptible		
Marquis mesothetic		1
Marquis susceptible	20.192*	
Kota resistant		-
Arnautka resistant	1	
Mindum resistant	241	
Mindum susceptible		i i
Khapli resistant	242	
Khapli susceptible	233	1
Arnautka susceptible		
Spelmar resistant	237	
Spelmar susceptible		
Khapli resistant	131	
Khapli susceptible		
Kota susceptible	244	
Little Club mesothetic		
Marquis resistant		
Kubanka resistant		1 1
Einkorn resistant	103	111, 138, 294
Einkorn susceptible		102
Kubanka mesothetic		69
Kubanka susceptible		
Marquis mesothetic	58	121
Marquis susceptible		121
Reliance resistant	161	21
Reliance susceptible		40
Little Club susceptible		
Marquis resistant		
Reliance resistant		
Kota resistant		
Arnautka resistant		
Attiautka iosistalit		

Table 3.—Key for identifying physiologic races of *Puccinia graminis* var. *tritici* on the basis of the reactions of 12 standard differential varieties of *Triticum spp.* — *Continued*

Physio Race Reaction of Differential Varieties number	(key Races with some similarities
Spelmar resistant	
Kubanka resistant	
Acme resistant	N N
Einkorn resistant	111 47, 50, 70, 71, 103
Einkorn susceptible	
Vernal resistant	102 104, 112, 160, 167, 180, 210, 229
Vernal susceptible	
Acme susceptible	
Vernal resistant	2 48, 59, 73, 162
Vernal susceptible	
Kubanka mesothetic	111.5
Acme resistant	
Einkorn resistant	195
Einkorn susceptible	
Vernal resistant	180 102, 112, 166, 167
Vernal mesothetic	
Vernal susceptible	
Acme mesothetic	50 47, 111, 139, 186, 204,
Acme mesometic	205, 206
A ama susaantihla	203, 200
Acme susceptible	120 50 196
Einkorn resistant	
Einkorn susceptible	59 2, 23, 48, 73, 162
Kubanka susceptible	
Acme resistant	2.4
Einkorn resistant	212
Einkorn susceptible	
Vernal resistant	
Vernal susceptible	211 181, 182, 224
Acme susceptible	:= -
Einkorn resistant	- 1'1 ·
Vernal resistant	186 50, 139
Vernal susceptible	27 197, 208
Einkorn susceptible	**
Vernal resistant	23 59, 118
Vernal susceptible	69 68
Spelmar susceptible	
Kubanka resistant	255
Kubanka susceptible	
Acme resistant	259
Acme susceptible	
Einkorn resistant	254
Einkorn susceptible	
Arnautka mesothetic	210
Mindum mesothetic	
Kubanka mesothetic	
	210 102 220
Acme resistant	
Acme mesothetic	47 16,50,111,204,205,206,225
Acme susceptible	107 27 200
Einkorn resistant	197 27, 208

Table 3.—Key for identifying physiologic races of *Puccinia graminis* var. *tritici* on the basis of the reactions of 12 standard differential varieties of *Triticum spp.* $\stackrel{.}{\rightarrow}$ *Continued*

Physiol Race (Reaction of Differential Varieties number	key Races with some similarities
Einkorn susceptible	.48 2, 14, 59, 73, 178
Arnautka susceptible	
Mindum resistant	2
Acme resistant	251
Acme susceptible	6 178
Mindum mesothetic	
Kubanka mesothetic	
Vernal resistant	
Vernal susceptible	209 45, 53, 119, 223
Mindum susceptible	
Spelmar resistant	256
Spelmar susceptible	
Kubanka resistant	- 1
Acme resistant	
Einkorn resistant	
Einkorn susceptible	223 45, 53, 209
Acme susceptible	
Khapli resistant	4
Khapli susceptible	252
Kubanka mesothetic	1 ° .
Acme mesothetic	.45 53, 119, 209, 223
Acme susceptible	,111 sec *
Einkorn resistant	
Einkorn susceptible	249 263
Kubanka susceptible	
Acme resistant	232 263
Acme susceptible	
Einkorn resistant	0.00
Vernal resistant	.16
Vernal susceptible	208 27, 197
Einkorn susceptible	
Vernal resistant	% 1
Khapli resistant	
Khapli susceptible	
Vernal susceptible	
Kota mesothetic	248
Kota susceptible	
Arnautka resistant	
Kubanka mesothetic	
Vernal resistant	140 105, 155, 203
Vernal susceptible	.65
Kubanka susceptible	
Vernal resistant	
Vernal susceptible	145
Arnautka susceptible	20
Mindum resistant	.28
Mindum susceptible	to be a set of
Spelmar resistant	247
Spelmar susceptible	
Kubanka resistant	220

Table 3.—Key for identifying physiologic races of *Puccinia graminis* var. *tritici* on the basis of the reactions of 12 standard differential varieties of *Triticum spp.* — *Continued*

Physiologic Race (key number)	Races with some similarities to those at left of vertical line
Kubanka susceptible	
Acme resistant258	
Acme susceptible	
Einkorn resistant207	
Einkorn susceptible	=
Vernal resistant19	78, 158
Vernal susceptible123	120
Reliance susceptible	
Kota resistant	
Arnautka resistant	
Kubanka resistant	
Acme resistant153	£
Acme susceptible7	152, 171, 175
Kubanka mesothetic	
Acme resistant66	
Acme susceptible	
Vernal resistant	7, 33, 171, 175
Vernal mesothetic175	7, 51, 152
Kubanka susceptible	,,
Einkorn resistant217	
Einkorn susceptible	
Vernal resistant33	152, 172
Vernal susceptible51	175
Arnautka susceptible	
Mindum mesothetic	
Vernal resistant151	1-10
Vernal susceptible89	83
Mindum susceptible	
Kubanka resistant	
Vernal resistant228	
Vernal susceptible257	
Kubanka susceptible	
Einkorn resistant95	
Einkorn susceptible	
Vernal resistant	96, 151
Vernal susceptible83	89
Kota susceptible	
Arnautka resistant	
Einkorn resistant	
Einkorn susceptible	
Vernal resistant177	
Vernal susceptible	
Arnautka mesothetic	39
Arnautka susceptible	
Mindum mesothetic	98
Mindum susceptible	20
Einkorn resistant98	63, 174
Einkorn susceptible	00, 1/7
Vernal resistant	38, 179
Vernal susceptible	50, 177

Table 3.—Key for identifying physiologic races of *Puccinia graminis* var. *tritici* on the basis of the reactions of 12 standard differential varieties of *Triticum spp.* — *Continued*

Reaction of Differential Varieties	Physiologic Race (key number)	Races with some similarities to those at left of vertical line
Marquis mesothetic		
Reliance resistant	*	
Kota resistant		
Arnautka resistant		
Kubanka resistant		
Acme resistant	-	
Einkorn resistant	-	
Vernal resistant	71	70, 111, 204, 206
Vernal mesothetic	70	71, 111, 204, 206
Einkorn susceptible		
Vernal resistant		102, 104, 112, 210
Vernal mesothetic		102, 227, 229
Acme susceptible	185	
Kubanka mesothetic		
Einkorn resistant	206	47, 50, 70, 71, 204, 205
Einkorn susceptible	'-	
Vernal resistant	112	43, 102, 180, 191, 227, 229
Vernal susceptible	181	182, 202, 211, 224
Kubanka susceptible		
Acme resistant	260	
Acme susceptible		23, 44
Arnautka mesothetic		
Einkorn resistant	205	47, 50, 204, 206
Einkorn susceptible		119, 202, 285
Arnautka susceptible		
Kubanka resistant	262	
Kubanka mesothetic		232, 249, 261, 268
Kubanka susceptible		
Einkorn resistant		
Vernal resistant	81	16, 75, 94
Vernal susceptible		184
Einkorn susceptible		
Vernal resistant	88	14, 24, 62, 91
Vernal susceptible		57, 117, 165, 190, 209
Kota mesothetic		
Arnautka resistant		
Kubanka mesothetic		
Acme resistant		total and the state of
Einkorn resistant	204	47, 50, 70, 71, 205, 206
Einkorn susceptible	168	202
Acme susceptible	162	1, 2, 59, 61
Kubanka susceptible		
Einkorn resistant	92	176
Einkorn susceptible		1, 61, 105, 140, 155
Arnautka mesothetic		2, 17, 37, 48, 59, 78
Arnautka susceptible		_,,,,,
Einkorn resistant	94	16, 21, 81
Einkorn susceptible		,,
Vernal resistant	261	263
Vernal mesothetic		9, 14, 85, 88, 120
Tornar mesothetic		1 -, 1 -, 05, 05, 120

Table 3.—Key for identifying physiologic races of *Puccinia graminis* var. *tritici* on the basis of the reactions of 12 standard differential varieties of *Triticum spp.* — *Continued*

	- *
Reaction of Differential Varieties Physiologic Race (key number)	Races with some similarities to those at left of vertical line
Kota susceptible	
Arnautka resistant	
Kubanka mesothetic	
Einkorn resistant	80
Einkorn susceptible	
Vernal resistant155	1, 61, 105, 140, 203
Vernal mesothetic105	57, 93, 140, 155, 203
Kubanka susceptible	1 ., , , , 2
Vernal resistant	1, 157
Vernal mesothetic157	57, 136, 154
Vernal susceptible	57, 157
Arnautka mesothetic149	9, 30, 76, 85, 120, 150, 156, 158, 194, 200, 201, 231
Arnautka susceptible	
Mindum mesothetic156 Mindum susceptible	9, 120, 149
Vernal resistant	17, 19, 73, 158
Vernal mesothetic	9, 19, 78, 120, 149
Vernal susceptible	9, 91, 123, 149, 156, 158
Reliance mesothetic	7, 71, 123, 147, 130, 136
Arnautka mesothetic	15, 108, 202, 219, 285
Arnautka susceptible	11, 14, 88, 96, 114, 179
Reliance susceptible	11, 14, 00, 90, 114, 179
Kota resistant	
Kubanka mesothetic171	7, 35, 74, 152, 172, 216
Kubanka susceptible	33, 35, 171
Kota mesothetic96	10, 11, 62, 179
Kota susceptible	10, 11, 02, 17
Arnautka resistant	
Vernal resistant	82, 84
Vernal mesothetic84	82, 193
Arnautka susceptible	1 10 10 10
Mindum mesothetic	
Vernal resistant	11, 179
Vernal susceptible106	15, 87
Mindum susceptible	
Einkorn resistant63	34, 98, 213
Einkorn susceptible	11, 39, 62, 96, 113
Marquis susceptible	
Reliance resistant	
Kota resistant	h-
Arnautka resistant	
Mindum resistant	
Spelmar resistant	
Kubanka resistant	
Acme resistant227	43, 104, 112
Acme susceptible	za skrainda - '
Vernal resistant54	ries ender
Vernal susceptible134	
Kubanka mesothetic43	112, 191, 227

Table 3.—Key for identifying physiologic races of *Puccinia graminis* var. *tritici* on the basis of the reactions of 12 standard differential varieties of *Triticum spp.* — *Continued*

Physiologic Race (key number)	Races with some similarities to those at left of vertical line
Kubanka susceptible	
Acme resistant191	43, 112
Acme susceptible	7.
Einkorn resistant	
Vernal resistant	
Vernal susceptible79	-
Einkorn susceptible	
Vernal resistant44	118
Vernal susceptible121	58
Spelmar susceptible283	
Mindum susceptible	
Spelmar resistant274	
Spelmar susceptible	
Kubanka resistant	
Acme resistant288	
Acme susceptible132	
Kubanka susceptible281	
Arnautka mesothetic	55, 165, 168, 181, 188
Arnautka susceptible	
Mindum resistant	
Kubanka resistant	142
Kubanka susceptible	
Acme resistant	165, 188
Acme susceptible273	100, 100
Mindum mesothetic	
Vernal resistant	24, 141
Vernal susceptible190	55, 117, 119
Mindum susceptible	33, 117, 117
Spelmar resistant	
Kubanka resistant	
Acme resistant	- ×
Acme susceptible289	
Kubanka susceptible	
Spelmar susceptible 203	
Kubanka resistant	
Acme resistant	
Einkorn resistant	*
	55
Einkorn susceptible	33
Acme susceptible	46 117 110 100 202
Kubanka mesothetic	46, 117, 119, 190, 202
Kubanka susceptible	
Acme resistant	
Einkorn resistant	262
Einkorn susceptible	263
Acme mesothetic	
Acme susceptible	F181.
Einkorn resistant	0.1
Vernal resistant	81
Vernal susceptible184	169

Table 3.—Key for identifying physiologic races of *Puccinia graminis* var. *tritici* on the basis of the reactions of 12 standard differential varieties of *Triticum spp.* — *Continued*

3, 142 5, 119, 190 66 29, 61, 149, 159, 200
5, 119, 190 16 29, 61, 149, 159, 200
5, 119, 190 16 29, 61, 149, 159, 200
5, 119, 190 16 29, 61, 149, 159, 200
29, 61, 149, 159, 200
29, 61, 149, 159, 200
29, 61, 149, 159, 200
29, 61, 149, 159, 200
29, 61, 149, 159, 200
29, 61, 149, 159, 200
29, 61, 149, 159, 200
29, 61, 149, 159, 200
29, 61, 149, 159, 200
29, 61, 149, 159, 200
7, 93, 124, 128
), 176
33
128, 155, 162, 203
7, 105, 159
, 100, 100
19
7, 159
, 139
9, 92, 198
9, 92, 176
1 120 126 155 162 20
1, 128, 136, 155, 162, 203
3, 105, 124, 154, 157, 159
9, 128, 149
7, 128, 149, 200
149
85, 149
85, 149
85, 149
85, 149
,

Table 3.—Key for identifying physiologic races of *Puccinia graminis* var. *tritici* on the basis of the reactions of 12 standard differential varieties of *Triticum spp.* — *Continued*

Reaction of Differential Varieties Physiologic Race (key number)	Races with some similarities to those at left of vertical line
Kubanka susceptible272	× .
Spelmar susceptible	
Acme resistant282	
Acme susceptible26	
Mindum mesothetic	
Kubanka mesothetic90	21
Kubanka susceptible	9, 149
Mindum susceptible	
Spelmar resistant	
Kubanka resistant292	
Kubanka susceptible	100
Acme resistant269	
Acme susceptible277	
Spelmar susceptible	
Kubanka resistant	
Acme resistant194	149
Acme susceptible	
Einkorn resistant276	
Einkorn susceptible	*
Vernal resistant5	37
Vernal susceptible8	
Kubanka mesothetic37	5, 17, 73
Kubanka susceptible	
Acme resistant279	
Acme susceptible	
Einkorn resistant	is in a
Vernal resistant21	90, 94, 161
Vernal susceptible116	170
Einkorn susceptible	1,00
Vernal resistant17	29, 37, 73, 78, 85, 114
Vernal mesothetic85	9, 17, 76, 91, 149
Vernal susceptible	3, 17, 70, 31, 113
Khapli resistant9	30, 76, 85, 91, 120, 149,
Knapn resistant	150, 156, 158
Khapli susceptible270	130, 130, 130
Reliance mesothetic	11, 17, 62
Reliance susceptible	11, 17, 02
Kota resistant	
Arnautka resistant	
Mindum resistant	
Kubanka resistant	
Kubanka resistant	
Einkorn resistant	215
Einkorn susceptible	213
Vernal resistant	35, 171, 216
Vernal susceptible	188, 219
Kubanka susceptible Kubanka susceptible	100, 219
Acme resistant	
Acme susceptible	
Einkorn resistant215	64
Ellikotti tesistatit213	1 04

Table 3.—Key for identifying physiologic races of *Puccinia graminis* var. *tritici* on the basis of the reactions of 12 standard differential varieties of *Triticum spp.* — *Continued*

Physiologic Race (key number)	Races with some similarities to those at left of vertical line
Einkorn susceptible	
Vernal resistant35	74, 171, 172, 216
Vernal susceptible219	108, 188
Mindum susceptible135	
Arnautka mesothetic	122
Arnautka susceptible	
Mindum mesothetic86	218
Mindum susceptible	X X
Spelmar resistant280	
Spelmar susceptible	
Acme resistant293	_
Acme susceptible	
Einkorn resistant	
Vernal resistant107	
Vernal susceptible143	129
Einkorn susceptible	127
Vernal resistant122	31
Vernal susceptible218	86, 163
Kota mesothetic	00, 103
Acme mesothetic	15, 32, 110, 199, 218
Acme susceptible	13, 32, 110, 133, 218
Einkorn resistant	40, 143
Einkorn susceptible	18, 35, 36, 74, 101, 171
Kota susceptible	18, 33, 30, 74, 101, 171
Arnautka resistant	
Mindum resistant	
Kubanka resistant	
	101
Acme resistant	101
Acme susceptible	
Einkorn resistant	
Einkorn susceptible3	36
Kubanka mesothetic	*
Acme mesothetic	56 125 126 106
Einkorn resistant127	56, 125, 126, 196
Einkorn susceptible	10.26.214.216
Vernal resistant	18, 36, 214, 216
Vernal susceptible67	52
Acme susceptible	
Einkorn resistant	
Vernal resistant125	56, 127, 146
Vernal mesothetic	97, 125, 147
Vernal susceptible97	146
Einkorn susceptible	1. 40.02.451.515
Vernal resistant36	3, 18, 82, 101, 216
Vernal mesothetic82	36, 52, 84, 193
Vernal susceptible52	67, 82
Kubanka susceptible	1 1 2 2 2 1 2 1
Acme resistant	
Einkorn resistant196	126, 127
Einkorn susceptible20	

Table 3.—Key for identifying physiologic races of *Puccinia graminis* var. *tritici* on the basis of the reactions of 12 standard differential varieties of *Triticum spp. — Continued*

Physiologic Race (key number)	Races with some similarities to those at left of vertical line
Acme mesothetic164	147
Acme susceptible	
Einkorn resistant	
Vernal resistant56	125, 127
Vernal susceptible147	146, 164
Einkorn susceptible18	36, 101, 216
Mindum susceptible	
Spelmar resistant25	
Spelmar susceptible22	
Arnautka mesothetic	
Kubanka mesothetic	
Einkorn resistant	34, 127, 192, 196, 213,
	222, 271
Einkorn susceptible32	11, 163, 199
Kubanka susceptible	22 1/2
Acme resistant	32, 163
Arnautka susceptible	
Mindum resistant	
Kubanka resistant	
Einkorn resistant	106 100
Vernal resistant271	126, 192
Vernal mesothetic	126, 271
Einkorn susceptible	
Mindum mesothetic87	15, 106
Mindum susceptible	
Spelmar resistant	
Acme resistant187	
Acme susceptible267	0
Spelmar susceptible	
Kubanka resistant	
Einkorn resistant222	126
Einkorn susceptible	
Kubanka mesothetic213	34, 63, 77, 100, 126
Kubanka susceptible	
Acme resistant100	213
Acme susceptible	
Einkorn resistant	
Vernal resistant34	63, 77, 126, 213
Vernal mesothetic77	34, 40, 213
Vernal susceptible40	77, 129, 144
Einkorn susceptible	, , , , , , , , , , , , , , , , , , , ,
Vernal resistant11	32, 62, 96, 110, 113, 114, 179
Vernal mesothetic110	11, 15, 163
	11, 13, 103
Vernal susceptible Khapli resistant15	87, 106, 110, 163, 188
Khapli susceptible189	07, 100, 110, 103, 188
Khaph susception107	
	1

Table 4.—Mean infection types produced by physiologic races of *Puccinia graminis* var. *tritici* on the standard differential varieties of *Triticum spp*.

•				D	ifferentia	ıl varieti	es and ir	ifection 1	types a			
Physio- logic Race ^b	Little Club	Marquis	Reliance	Kota	Arnautka	Mindum	Spelmar	Kubanka	Асте	Einkorn	Vernal	Khapli
	4	4-	0	3+	1 =	1	1 =	3+	3++	3	0;	1 =
	4	2=	2 =	2=	1-	1	1 =	1+	3++	3+	1-	0;
	4	4–	4=	3+	1 =	1 =	1-	1+	3++	3+	1 =	0;
	4+	2-	1-	2=	4=	3+	3++	2	3++	3++	1 =	1 =
	4	4–	0;	3	4=	3++	3++	1++	3+	3	0;	0;
	4	2	1 =	0;	3+	2=	2=	1	3+	3	0;	0;
	4	2=	3+	1 =	1 =	1++	1-	1	3++	3-	1	1-
	4	4	0;	4–	4=	3++	4=	0;	3	3	4	0;
	4	4– 2–	0	3++ 2	4-	4=	4=	4=	3++	3+	4±	1-
*11.	4+	2- 4=	3++	3+	4	4	4	3++	4-	3+	l =	1 =
	4- 4+	4 = 4-	3++ $4=$	3+ 3+	4 = 4 =	4 = 1	4=	3++	3++	$\frac{3}{3++}$	1 = 1 =	1 =
13.		4-	3++	3+ $3++$	4=	3++	1++ $3++$	1++ 2-	3++ 3++	3++	1 =	0; 1 =
	4 ₊	2-	1-	1++	3++	3++	3++	3++	3++	3	1 =	0;
*15.		4-	4=	3++	4=	4 ±	4=	3++	3++	3++	$4\pm$	0, 1 =
	4–	2=	0	1	3++	3+	3++	3++	4 =	1 =	1 =	1
17.		4-	0;	3+	4=	4=	4=	3++	3++	3	1=	1 =
18.		4–	4=	3++	1	1 =	1-	3++	3++	3+	1-	1 ±
19.		2-	0;	3-	4=	4=	4=	3++	3++	3	0;	1 =
20.		4=	4=	4 =	1++	1-	1++	3++	1++	3+	1 =	1-
*21.		4	0	3++	4-	4-	4-	4=	3++	1 =	0;	1 =
22.	4+	4+	4	3	1	4	4–	0;	3+	3	1-	0;
23.	4	2	1-	1 =	1	1 =	1-	3+	3++	3	0;	0;
*24.		4 =	0;	2=	4=	4=	4=	3++	3+	3+	1 =	0;
25.		4	3+	3	1 —	3	1 =	3	3++	3	1 =	1-
26.		4	0;	3	4–	1 =	3++	1 =	4=	3	1-	1+
	4=	2	O	0;	1 =	1	1-	4=	3++	1 =	$4\pm$	1 + +
28.		2	0;	3	4-	1	4=	3	3	3	1 =	0;
*29.		4–	0	3	X++		X+	X	X+	3	1-	1 –
30.		4	0;	3++	X++		X +	$X \pm$	X++		4=	1
	4+	4	3++		X-				$X \pm$		1-	1
	4	4=	4=	3+		X±	$X\pm$	X-	X_{+}		1 =	1-
	4+	2	4		1 =	1-	1	4=	3++		1-	1
	4+	4-	4-	4=	4	4=		4±	3++		0;	$1\pm$
35.		4 = 4	3+	0;	1 =	1-		3+ V	3++		0;	1
	4 4	4 4-	4– 0	3++	1 =	1 = 4 =	0;	X			0;	1-
*38.		2=	4-		4=X+	4 = X±		$X_{\pm} \ X_{+}$	3+ $X++$		1 = 1 =	1- 1+
	4–	2= $2=$	4=	3+	4 ₊	3++		4=	3++		1 = 1 =	1-
		<u> </u>	7=	J+	7+	7++		Τ≓	7++	7=	1 =	

Table 4.—Mean infection types produced by physiologic races of *Puccinia graminis* var. *tritici* on the standard differential varieties of *Triticum spp.—Continued*

				D	ifferenti	al varieti	es and ir		types a			
Physio- logic Race ^b	Little Club	Marquis	Reliance	Kota	Arnautka	Mindum	Spelmar	Kubanka	Асте	Einkorn	Vernal	Khapli
40	.4+	4+	4	4+	4+	4+	4	4=	4	0;	4=	1 =
41	.2++	4	O	0;	4=	4	4+	4+	4–	4-	1-	$4_{\rm c}$
42		4	$1 \pm$	0;	4+	4	4	4	4	4=	2 =	$4_{\rm c}$
43		3++	0	0;	0;	0;	0;	X	1	3	1	0;
44		3++	O	0;	0;	0;	0;	3+	3+	3	1	0;
*45		2	0	2-	4	4	4	X	X	3	3	1
46		3 + +	0	2-	4	4	4	1	1	3	3	1
47'	.4	2-	0	$1\pm$	X-	X;	X++	X;	$X\pm$	1 =	0;	1 =
*48	.4+	1	0;	1+	X+	X =	$X\pm$	X+	4-	4=	1 =	1+
*49		4-	O	4=	1 =	1-	0;	X =	3+	1-	0;	1 =
50	.4+	2+	0;	2++	1-	0;	0;	X =	$X\pm$	0;	0;	0;
51	.4	2=	3+	0;	0;	0;	0;	4	3++	3+	4-	0;
52		4	4-	4	1 =	1 =	1 =	$X\pm$	4	4-	4+	1-
*53	.4	$2\pm$	O	1	4	4	4	4	4	$3\pm$	$3\pm$	1
54	.4	3++	O	0;	0;	0;	0;	1	3+	3	1	0;
55		4	0	2-	4	4	4	X	X	3	3	1
*56	.4	3+	3+	3+	1 =	1 =	1 =	3+	3+	1 =	1 =	1-
57	.4	4-	0;	3+	1	1	1	4	3+	3	3	1
58	X +	X+	O	0;	1+	1 =	$1\pm$	4+	3+	3++	4+	1 + +
*59	.4+	2+	0	0;	1 =	1 =	1 –	X-	3++	3+	1 =	0;
60	.4++	4++	0;	3++	0;	0;	0;	0;	3+	$1 \pm$	0;	1 =
61	.4+	4	O	3+	0;	0;	0;	X	4+	4	0;	0;
62	.4	$X\pm$	X+	X	4	4	4	4	4	3++	0;	1 –
63	.4+	X + +	4	3++	4+	4++	4+	4+	4n+	1 =	1 =	0;
64	.4++	4+	3++	$1 \pm$	1 =	0;	1 =	$X \pm$	3c+	1 =	0;	1
65		2	0	3	0;	0;	0;	X	4	4	4	1
66		2	4	0;	0;	0;	0;	X+	1 =	3	O	O
67		4+	4	4	$1\pm$	2 =	2=	X =	X+	3-	$4\pm$	1 –
	X+	2+	0	0;	1 =	1+	1 –	X++	$4\pm$	4	4++	0;
*69	.3++	2+	0;	0;	0;	0;	0;	3+	4=	3	3++	1 =
70	.4+	X+	0;	0;	0;	0;	0;	0;	0	1 =	$X \pm$	0;
71		X-	0	0;	0;	1 =	0;	1 =	0;	0;	0;	0;
72		2	0;	0;	$1\pm$	1+	1+	4+	4+	3+	$3\pm$	X
73		X	0	X	X	X	X	X	$3\pm$	4–	1	1
74		4–	3=	2+	0;	0;	0;	Х-	3+	$3\pm$	0;	1
75		3+	2+	0;	3+	3+	3+	4–	3+	1	0;	1
76		4–	0	3+	X	X	X	X	3+	3+	X-	1
77		4	3=	3-	3-c	3-c	3-c	4–	3+	1±	X	1
78	.4	X	0	3=	3-c	3-c	3-c	3+	3+	3+	1	1

Table 4.—Mean infection types produced by physiologic races of *Puccinia graminis* var. *tritici* on the standard differential varieties of *Triticum spp.—Continued*

$\begin{array}{cccccccccccccccccccccccccccccccccccc$					D	ifferentia	al varieti	es and in	nfection	types a			
804	logic	Little Club	Marquis	Reliance	Kota	Arnautka	Mindum	Spelmar	Kubanka	Acme	Einkorn	Vernal	Khapli
814			4-	0	1 –	1 –	1 –	1-	4-		0;	3+	1
824	80	4	3-e	O	3-	0;	0;	0;	X-	3+	1-	3+	1
834			X	O		4					1-		1-
844 X 3-c 3- 0; 0; 0; X 4 3+ X 1 854 4- 0 3± 4- 4 4 4 4 4 3+ X 1 864 3+ 3+ 1± 3+ X X X X 3+ 3+ 3+ 1 *874 4 4 3± 4 X X X X 3+ 3+ 3+ 1 884 X 0 1± 4 4 4 4 4 3± 3+ 1 1 894 2 3+ 0; 4 X X X 3± 3+ 3+ 1 1 1 1 1 914 X 0 X 4 4 4 4 4 3+ 1 1 1 914 X 0 X 4 4 4 4 4 1 1 1 934 3+ 0 3= 0; 0; 0; X 3± 3+ 3+ 1 944 X 0 X 4 4 4 4 3+ 1 1 1 934 3+ 0 3= 0; 0; 0; X 3± 3+ 3+ 1 944 X 0 X 4 4 4 4 3+ 1 1 1 954 2 3± 0; 4 4 4 4 3+ 1 1 1 964 X 0 X 4 4 4 4 3+ 1 1 1 974 3+ 4 3+ 0; 0; 0; 0; X 3± 3+ 3+ 1 991+ X 3+ 3 0; 2+ 2+ 4+ 2+ 2+ 3+ 3+ 1003± 4 3+ 3+ 3 0; 2+ 2+ 4+ 2+ 2+ 3+ 3+ 1003± 4 3+ 3+ 3= 3 3- 3= 4= 1 1± X± 1 1014+ 4++ 4- 4± 1 0; 0; 0; X+ X- 3 0; 1± 1024± 0; 1+ 0; 0; 0; 0; X- 3+ 3 X 1= 103X++0 0; 0 0 0 0; 0; 0; 0; 0; 0; 0; 0; 0; 0;			3+	3+	3+	0;		0;	X			X	1
854 4- 0 3± 4- 4 4 4 3+ X I 864 3+ 3+ 1± 3+ X X X 3+ 3+ 3+ 1 *874 4 4 3± 4 X X X 3+ 3+ 4 1 884 X 0 1± 4 4 4 4 3+ 1 1 894 2 3+ 0; 4 X X X 3+ 3+ 1 1 904 4 0 3± 4 X X X 3+ 3+ 1			1+	3-		3+	3+	3+	3+	3+	3+	3+	1
864 3+ 3+ 1± 3+ X X X 3+ 3+ 3+ 1 *874 4 4 3± 4 X X X 3+ 3+ 4 1 884 X 0 1± 4 4 4 4 3+ 3+ 1 1 894 2 3+ 0; 4 X X X 3± 3+ 3+ 1 1 904 4 0 3± 4 X X X 3± 3+ 3+ 1 914 X 0 X 4 4 4- 3+ 3+ X 1 924 X 0 X 1 1 1 4 4 1 1 1 934 3+ 0 3= 0; 0; 0; X 3± 3+ 3+ 1 1 1 954 2 3± 0; 4 4 4 <	84	4		3-c		0;	0;	0;					1
*874	85	4		0	$3\pm$	4–	4	4	4	4		X	1
$\begin{array}{cccccccccccccccccccccccccccccccccccc$			3+	3+	$1 \pm$	3+			X	3+	3+	3+	1
$\begin{array}{cccccccccccccccccccccccccccccccccccc$			4	4	$3\pm$	4		X		3+	3+	4	1
$\begin{array}{cccccccccccccccccccccccccccccccccccc$													1
$\begin{array}{cccccccccccccccccccccccccccccccccccc$			2	3+	0;	4	X	X		$3\pm$	3+	3+	1
$\begin{array}{cccccccccccccccccccccccccccccccccccc$	90	4	4	O	$3\pm$	4	X	X	X	3+	1 .	1	1
$\begin{array}{cccccccccccccccccccccccccccccccccccc$	91	4	X	O	X	4	4	4	4–	3+	3+	X	1
$\begin{array}{cccccccccccccccccccccccccccccccccccc$	92	4	X	O	X	1	1	1	4	4	1	1	1
$\begin{array}{cccccccccccccccccccccccccccccccccccc$	93	4	$3 + 10^{-1}$	O	3 =	0;	0;	0;	X	$3\pm$	3+	3+	1
$\begin{array}{cccccccccccccccccccccccccccccccccccc$	94	4	X	O	X	4-	4-	4–	4–	3+	1	1	1
$\begin{array}{cccccccccccccccccccccccccccccccccccc$	95	.4	2	$3\pm$	0;	4	4	4	4	3+	1	1	1
$\begin{array}{cccccccccccccccccccccccccccccccccccc$	96	4	X	4		4	4	4	4	3+	3+	1	1
$\begin{array}{cccccccccccccccccccccccccccccccccccc$	97	4	3+	4	3+	0;	0;	0;	X	3	0;	3+	1
$\begin{array}{cccccccccccccccccccccccccccccccccccc$	98	4	2=	4+			3++	3	4=	3-	$1\pm$	1	1-
$\begin{array}{cccccccccccccccccccccccccccccccccccc$			X	3++	3	0;		2++	4+	2+	2+	3++	3++
$\begin{array}{cccccccccccccccccccccccccccccccccccc$	100	3±	4		3=		3-		4 =				
$\begin{array}{cccccccccccccccccccccccccccccccccccc$	101	.4+	4++	4-	$4\pm$	1	0;	0;	X_{+}	X-	3	0;	$1 \pm$
$\begin{array}{cccccccccccccccccccccccccccccccccccc$	102	4±		1+	0;	0;	0;	1 =	1 =	0;	3+		1 =
$\begin{array}{cccccccccccccccccccccccccccccccccccc$	103	X+-	⊢ 0	0;		0	0;	0;	0;		2-	1 =	0;
$\begin{array}{cccccccccccccccccccccccccccccccccccc$	104	4	X =	O	0;	0;	0;	0;	0;	0;	3+	X+	0;
$\begin{array}{cccccccccccccccccccccccccccccccccccc$	105	4	X-	O	$3\pm$	0;	0;	0;	X-	3+		X	
$\begin{array}{cccccccccccccccccccccccccccccccccccc$	106	4	X	3	3-		X	X	X	3	3+	4-	1 –
$\begin{array}{cccccccccccccccccccccccccccccccccccc$	107	4	$3\pm c$	3-	0;	4	4	4	4	3		0;	1-
$\begin{array}{cccccccccccccccccccccccccccccccccccc$			4	4-		1 ±	0;	0;	X_{+}		3		1-
$\begin{array}{cccccccccccccccccccccccccccccccccccc$			$2\pm$	4						3-			1
$\begin{array}{cccccccccccccccccccccccccccccccccccc$													
$\begin{array}{cccccccccccccccccccccccccccccccccccc$													
$\begin{array}{cccccccccccccccccccccccccccccccccccc$													
1144 $3+$ X $3+$ 4 4 4 $4 3+$ $1 1$													
1154 $2 3=$ $3=$ $4 4 4 4 4 3+$ $3\pm$ $1-$			2-	3=	3=	4-	4-	4	4–	4–	3+	$3\pm$	1-
1164 4- 0 3 4 4 4 4 4- 1 4- 1-				0	3	4	4	4	4	4–			
1174 4- 0 0; 4- 4- 4- 4- 4 3+ 3+ 1-			4-	0	0;	4-	4-	4-	4-	4	3+	3+	

Table 4.—Mean infection types produced by physiologic races of *Puccinia graminis* var. *tritici* on the standard differential varieties of *Triticum spp.—Continued*

	Differential varieties and infection types ^a													
Physio- logic Race ^b	Little Club	Marquis	Reliance	Kota	Arnautka	Mindum	Spelmar	Kubanka	Acme	Einkorn	Vernal	Khapli		
118		X	0	1-	1-	1-	1-	4	4	3+	1-	1-		
119		X	0	0;	4	4	4	4	4-	3+	3+	1-		
120		X	0	3 =	4	4	4	4	4–	3+	3	1-		
121		4-	O	0;	1-	1-	1-	4	3+	3	3+	1		
122		3+	4-	0;	4	4	4	4	4–	3+	1-	1		
123		2-	0	3-	3+	4-	4	4	4-	3+	3+	1		
124		3-c	O	3 = c	0;	0;	l =	3+	X	3	X-	1		
125		4	4	4	0;	0;	0;	X	4	1 =	0;	1 –		
*126	.4=	4 =	3+	3+	$X\pm$	X++	X+	X-	X	$1\pm$	1 =	1-		
127		4–	3 + +	3+	1 =	$1\pm$	1 =	\mathbf{X}	X	0;	0;	1-		
128		3++	0;	$3\pm$	1 –	1 =	1	X-	$X\pm$	$3\pm$	1 =	1-		
129		4	4	X	4	4	4	4	4	1-	4	0		
130		2	0	O	4	4	4	4	4	3+	O	1-		
131	.1-	4	0	O	4	4	4	4	4	4+	1	1 –		
132	.4	4	O	2	1	4	4	1	4	1	1	1		
133	.4	4	O	O	1	2	2	4	4	0	1	2		
134		4	O	0;	0;	0;	0;	1	3	3	3	1		
135	.4	4	4	0;	0;	3	2	4	3	1	1	1		
136	.4	X	O	3 =	0;	0;	0;	4-	4	4-	1-	1		
137	.4	4-	4-	0;	1-	1 –	1-	3	1 –	3-	X-	1		
138	.2	0;	O	0;	0;	0;	0;	0;	0;	1+	Х-	0;		
*139	$.4 \pm$	2+	1-	$2\pm$	1 –	1 =	1	X	4+	1=	1-	0;		
140	.4+	2-	1	4=	$1 \pm$	0;	$1\pm$	X+	$4\pm$	4-	$1\pm$	$1 \pm$		
141	.4	4	1+	O	4	1 –	4	1+	4	4	1-	1+		
142		4-	2	O	3++	X	4	X+	4	4	1	1 + +		
143	.4	4-	4-	O	4-	4–	4–	4-	3++	2	3++	1 =		
144	.X	4	4	3+	4-	4–	4–	4–	3++	1+	3++	1 + +		
145	.4	0	2	4	0;	0;	0;	4	4	0;	4	2		
146	.4+	4	$4\pm$	3++	1 –	$1 \pm$	1 =	$X\pm$	3++	1 =	$X\pm$	1+		
147	.4++	4+	4	$4\pm$	1 =	1-	1	4+	4	1 =	$4\pm$	$1 \pm$		
148	.4	3+	3+	3+	1-	0;	0;	0;	$3\pm$	1-	0;	1-		
149	.4	X+	O	3-	X+	X	X	X	X	X	X	1-		
150	.4	3-	O	3-	3+	X	X	4-	X	3+	3+	1 –		
151	.4	1	3-	0;	4-	X	X	X	4-	3+	0;	1 –		
152	.4	1+	3-	0;	1	0;	0;	X-	3+	3+	0;	1 –		
153		1+	3	0;	0;	0	0	0;	0	0;	Х-	0;		
154	.4	X	0 .	3=	1	0;	0;	4	4	$3\pm$	4-	1		
155	.4	X	0	3=	1	0;	0;	X	4	3+	0;	1		
156	.4 .	X	0	3=	4	X	X +	3+	4-	$3\pm$	4-	1		

Table 4.—Mean infection types produced by physiologic races of *Puccinia graminis* var. *tritici* on the standard differential varieties of *Triticum spp.—Continued*

-		Differential varieties and infection types ^a													
hysio- logic Race ^b	Little Club	Marquis	Reliance	Kota	Arnautka	Mindum	Spelmar	Kubanka	Acme	Einkorn	Vernal	Khapli			
157.	4	X	0	3=	1-	0;	0;	4	4	3+	X	1-			
158.		X	0	3 =	4	4–	4–	4–	4–	3+	X	1			
159.	4–	4	0	3++	1	1 =	1 =	X++	X	4=	$X\pm$	1			
160.	$X\pm$	0;	O	0;	0;	0;	0;	$1 \pm$	0	3+	1	0;			
161.	X	4	O	3++	4=	4-	4–	4=	3++	1 =	0;	0;			
162.	4	$X \pm$	0;	Х-	0;	0;	0;	X	3	3	0;	1			
163.	4–	4=	4-	X	4-	4	4	4-	\mathbf{X}	3++	$X\pm$	1 =			
164.	4	4-	4=	3+	0;	0;	0;	3++	X =	1-	3+	0;			
165.	4	$X\pm$	2	0;	X-	X-	X =	$X\pm$	X =	3	4-	$1 \pm$			
166.	4-	1 + +	$2\pm$	0;	1 =	0;	0;	4–	0;	3+	1 =	1 –			
167.	4	2-	2++	1-	0;	0;	0;	X	0;	3++	X	1			
168.	4	X	O	X	0;	0;	0;	X	0;	3	3+	1 =			
169.	4	X	0	0	4	4	4	4	4	0;	3+	1			
170.	4	4	1	X	4	4	4	4	4	0;	4	1			
171.	4	$X\pm$	3-	0;	1	0;	0;	X-	3+	3+	0;	1-			
172.	4	X	3-	2-	1-	0;	0;	4-	4	3	0;	1 –			
173.	4	2	4-	3-	0;	0;	0;	4	4–	1 –	0;	1			
174.	4	2	4-	3 =	4-	X	X	4-	4-	1 –	0;	1			
175.	4	2+	4	1 ±	1-	0;	0;	X	4-	$3\pm$	X	1-			
176.	4	4	O	4-	1-	1-	1 –	4	4-	1	0;	1-			
177.	4	2	4-	3-	1-	1-	1-	4–	3+	3	0;	1 –			
178.	4	1	0;	0;	4	X-	X	X+	4	3+	0;	1			
179.	4	X	4	4-	4	4	4	4	4–	3+	1-	1 –			
180.	4+	2=	0;	1 =	$1 \pm$	1 =	1-	$X \pm$	1 =	3+	0;	$1 \pm$			
181.	4	X+	0;	0;	0;	0;	0;	X	1 –	$3\pm$	3+	0;			
182.		2++	$2\pm$	0;	1 + +	$1\pm$	1	$X\pm$	1	3	3	$1 \pm$			
183.	4	X	O	3=	1-	0;	0;	X	4-	1 –	4–	1-			
184.	4	3	O	0;	3	3	3-	4=	4	1	4	1			
185.	4	Х-	O	0;	1 =	0;	. 1 =	1 =	4	1 =	0;	1			
186.	4	1	0	0;	1	0;	0;	4=	4=	1	0;	1			
187.		4	3	3	4-	3++		1 + +	1++	0	2	1			
188.	4	X+		$X\pm$		X++		X+		3+	3++	$1 \pm$			
189.	4	4	4	3+	4	4	4	4	4	4	4	4c			
190.	4	4-	0;	0;	4 =	X +	Х-	X	$3\pm$	3	3+	0;			
191.	4	3++		1+	0;	0;	0;	4=	0;	3+	0;	1			
192.	4	4-	4–	4-	4	0;	0;	0;	$3\pm$	1	X-	1			
193.	4	\mathbf{X}	4-	3	0;	0;	0;	X	4	3+	0;	1			
194.	4	4-	0	3++	4	4	4		0;1ь	0;1-	0;1-	0;1			
195.	4	2=	O	0;	1 –	0;	0;	X++	. 1-	1 + +	3+	2=			

Table 4.—Mean infection types produced by physiologic races of *Puccinia graminis* var. *tritici* on the standard differential varieties of *Triticum spp.—Continued*

		•			Differen	itial vari	eties and	Infectio	n types	a		
Physio- logic Race ^b	Little Club	Marquis	Reliance	Kota	Arnautka	Mindum	Spelmar	Kubanka	Асте	Einkorn	Vernal	Khapli
196		3+	3+	3+c	1-	1-	1-	3+	0;	1	1-	1-
197		2	0	1 –	X	X	X	X +		1-	4	1 –
198		4	0	3+	0;	0;	0;	4	3+	1-	X	1-
199		3+	3+	3+	X_{-b}		X_{-b}		0;	3	1 –	1 + +
200		3+c	0	3+		+bX+			1 –	' 3	1-	1-
201		3+	0	3++		1 –	1-	3+	0;	1 –	1-	2-
202		3+	2	0;	X	X	X	3+	0;	3	3+	1 –
203		X	0	X	0;	0;	0;	3+	3+	3	0;	1-
204	4	X	0	X	0;	0;	0;	Х-	1-	1 –	0;	2-
205 206		X X	0	0;	X_b	X_b	X_b	3+	0;	0;	0;	0;
207		2-	2	1-	0;	0;	0;	X	0;	1-	0;	2-
208		2- 2-	0	3-	4	4	4	4	4	1-	1-	1-
209		2 -	0	$\frac{1\pm}{2}$	3+	3+ V	3+	3+	3+	1-	3+	1-
210		2	2		3+	X	X	X-	3+	3	3+	1 ±
211		2-	0	0; 1±		+ X=	X =	X	1-	3	1-	1++
212		2-	0	2-	0; 1-	0; 1-	0; 1-	3+	0;	3++	3+	1++
213		4	3	3	4	4	1 – 4	4 X	$1\pm X$	1-	1-	1-
214		3	3	3	0	0	0	0	0	1 3	0	0
215		4	3	2	0	0	0	3	3	0	0	0
216		4	4	X	2	2	2	4	3 4	3	0	0
217		2	3	0	0	0	0	4	4	0	3	0
218		3	3	0	3	3	3	3	3	3	3 4	0
219		4	3	0	2	2	2	3	3	3	3	0
220		2	0	3	4	4	4	1	1	4	4	0
221		3	0	3	0	0	0	1	1	1	0	0
*222		3	3	3	3	3	3	1	1	0	0	0
223		2	0	0	3	3	3	0	0	3	3	0
224		2	0	0	2	2	2	1	1	3	3	0
225		2	0	0	3	3	3	1	1	1	0	0
226	4	3	0	0	3	3	3	0	0	0	0	0
227	4	3	0	0	0	0	0	1	1	3	0	0
228	4	2	3	0	4	4	4	1	1	3	0	Ö
229	4 n	X	0	0	0	0	0	1	1	3	0	0
230		2	0	O	0	0	0	0	3	3	3	0
231		4	2-	3 =	3	0;	0;	1	3	1	0;	1
232		$2\pm$	0	1-	$4\!\pm\!{}_{b}$	$4\pm b$	$4\pm b$	$4\pm b$	0;	3	1-	1
233°		4	0;	0;	0;	3	1	2	4	4	0	4
234	0	0	0	0	2-	3	2+	2-	0	1-	0	0

Table 4.—Mean infection types produced by physiologic races of *Puccinia graminis* var. *tritici* on the standard differential varieties of *Triticum spp.—Continued*

	Differential varieties and infection types ^a												
hysio- logic Race ^b	Little Club	Marquis	Reliance	Kota	Arnautka	Mindum	Spelmar	Kubanka	Acme	Einkorn	Vernal	Khapli	
235	.1++	1++	1++	1++	3 =	1++	1-	1-	1	1+	1++	3 =	
236		2	1+	2++	3-	3	3	1++	3	O	O	0	
237	.1+	3-	1 +-	2-	3-	3-	1 + +	3-	3 =	2=	1 =	1 =	
238	.1	1+	O	3-	1	1	1	1	1	O	1	3	
239	.1++	2	1	1	2	1+	1 + +	3-	3-	3	1	1 + -	
240		2-	0;	2	3 =	3	2	2+	0	0;	0	0	
241	.2+	4	0	2+	2++	2 + +	2++	4	2++	0;	0;	0	
242		3=	0	2==	2 =	3 =	1	3=	3 =	1-	0	1	
243		0	0 .	2=	1 =	1++	3 =	1+	1+	1	O	1+	
244		4	O	3	4	4	3++	3	3++	2	1	2-	
245		2	0;	0;	4	4	4	4	4	4	0;	4	
246		$\frac{1}{1}$	1+	0;	0;	4	4–	4	4–	3++	1	0;	
247		0;	0;	3+	4-	4	2+	4–	4	3-	1+	1+	
248		0;	0;	X.	0;	4-	4_	4-	4	4	1	1	
249		1	0;	0;	4	4	4	X	4-	4-	1	X-	
250		1	0,	3	2+	3+	3-	3+	3-	1	0;	0;	
251		2+	0	0	3+	0	1	0	3– 1		1	1	
			0	0	3+ 4-	3			3	1+		4-	
252		1+					3+	2+		3-	0;		
	.3++	1+	2	2+	4	4	4	X	4	2-	0;	0;	
254		1++	1 =	1	1++	1+	3=	3=	3 =	1-	0	0	
255		0	0	0	2-	4=	4–	0	0	0	0	0	
256		1-	0	1++	3	4	1	1	3=	3	1	2	
257		2	3	1	3	3	3	1	0	0	3	3	
258		2+	1 =	4	4	4	4–	4=	1+	1	0;	1	
259		1	O	1	1+	3 ==	3-	3-	1	2-	0	O	
260		X	0;	0;	0;	4–	3+	4	0;	4–	-1	0;	
261		X	0;	X	4–	4	4–	4	4-	4-	1+	2-	
262		X	0;	0;	3+	4-	4	2++	4-	4	3+	3-	
263	.3+	X	0;	0;	4-	4-	4–	X	X	3 + +	1	2 =	
264		4	0;	4	0;	4	4	4	4	4	0;	0;	
265	.4	4-	0;	0;	3++	4	0;	4–	4–	4	1-	1 –	
266		4-	0;	1 =	4=	4	4-	4-	X	0;	0;	1-	
267		4	4	4	3	3	2	2	3	0;	4	4	
268		4	0	2	4	3	4	4	2+	3-	1	0;	
269		3	0	4-	4-	4	0	4	0	1-	1-	0	
270		4	1+	4	3+	3++	4	4	4	4	3+	3+	
271		4–	3	4–	4	1	0	1	4–	2±	1	1+	
272		4-	0	4	4	2	0	4	2++	2+	1	2-	
273		3	0	1++		2	3	3+	3++		0;	0	

Table 4.—Mean infection types produced by physiologic races of *Puccinia graminis* var. *tritici* on the standard differential varieties of *Triticum spp.—Continued*

-				D	ifferenti	al varieti	es and i	nfection	types a			
Physio- logic Race ^b	Little Club	Marquis	Reliance	Kota	Arnautka	Mindum	Spelmar	Kubanka	Асте	Einkorn	Vernal	Khapli
274	.4–	3-	0	1++	2	3	1+	3	3-	1	0;	1
275	.4	4	0	2	3+	3+	3 =	1+	3	1-	0;	0;
276	4-	3=	O	3 =	4	3+	3 =	1++	3-	1	1	1
277	3 +	3-	O	3-	3-	3-	1++	3=	·3=	1+	0;	1-
278	3+	3	O	1+	3	3++	3	3+	1++	1 –	0;	1-
279	3	3+	O	3	3+	3+	3	3=	1++	1	1 –	0;
280		3+	3 =	$1\pm$	3 =	3 =	1 + +	1+	1-	1-	0	0
281		3-	0	2-	1++	3	3-	3=	3 =	0;	0;	0;
282	3 =	3 =	1 –	3-	3 =	1+	3 =	1 –	1	1 =	1	1
283		4–	O	O	1-	1 –	3	4	4–	2	1	1
284		3=	4	O	0	O	0	O	4	0;	0;	1 2
285 ^d		4	O	1	3+	1-	0	4	1	1	0;	0;
286		3	O	3 =	1+	3 =	1 + +	1+	1+	1	1	1
287		4	0	3+	2	2	4	4	2	1	1	O
288		3+	O	1+	1 + +	4–	3	1 + +	1++	1	1	0;
289		3	0	1	3+	3+	1	0	3++	1	0	O
290		4	0	3+	0	4+	4+	4	3+	0;	0;	0;
291		3 .	0	2	3 =	3	1+	1	1+	2-	1	1
292		3	0	3	3	3	O	1 + +	1	0	1	1
293		3	3-	2	3-	3+	4	4-	2-	0;	0;	0;
294 295-29		1	0	1++	2	2	2=	1++	2	1	0	0

^a The mean infection types are those which have been most commonly observed under a normal range of environmental conditions. The type may vary somewhat with different isolates and can vary considerably with environmental conditions, especially for certain race-variety combinations.

bThose races marked with an asterisk* have been subdivided. It is known that most of the races that have been studied extensively can be subdivided, and it is probable that most of those which have been prevalent in nature can be subdivided.

^cThe infection types given for races 233-294 deviate slightly from the originals sent the writers by Prof. C. Sibilia of Italy. In the original, a semicolon (;), indicating the presence of flecks, was sometimes placed after infection types I and 2. The semicolon has been retained only after zeros, in accordance with the infection types described in table 2.

^dThe infection types listed here are considered authentic for race 285, by agreement between Prof. C. Sibilia, Rita Basile, and the authors. The types recorded by Levine and Basile for 285 (See reference) are really those of race 133, which is due to an oversight by Stakman and Stewart in assigning race numbers.

eSee footnote h, table 5.

Table 5.—Country, year, and identifier of original collections of races 1—297 of *Puccinia graminis* var. *tritici*.

Races ^a	Country of Original Collection b	Year ^c	Identified by ^d
1-26	USA	1917-19	Minnesota
27	France (J. Dufrenoy)	1919	Minnesota
28-31	USA	1918-19	Minnesota
32	Canada (W. P. Thompson)	1918	Minnesota
33	USA	1920	Minnesota
34	South Africa (G. F. Puttick)	1921	Minnesota
35-38	USA	1921-22	Minnesota
39	Mexico	1923	Minnesota
40-42	Egypt (Tewfik Fahmy)	1924	Minnesota
43-46	Australia	1921-22	W. L. Waterhouse
47	USA	1929	Minnesota
48-49	Canada	1926	M. Newton and T. Johnson
50-52	USA	1927	Minnesota
53	Canada	1927	M. Newton and T. Johnson
54	Australia	1922-23	W. L. Waterhouse
55	Australia	1921-22	W. L. Waterhouse
56	USA	1928	Minnesota
57*	Canada	1927	M. Newton, T. Johnson,
51	Canada	1721	and A. M. Brown
58	Portugal	1928	M. Bensaude
59	USA	1929	Minnesota
60	USA (mutant of race 1)	1928	Minnesota
61-62*	USA	1928	Minnesota
63-64	Canada	1928	M. Newton and T. Johnson
65	Mexico	1929	Minnesota
66*	USA	1929	Minnesota
67-72**	USA .	1930	Minnesota
73-75	Canada	1928	M. Newton and T. Johnson
76**	Canada	1928	M. Newton and T. Johnson
77-78	Canada	1929	M. Newton and T. Johnson
79-81**	Canada	1928	M. Newton and T. Johnson
82**	Canada	1930	M. Newton and T. Johnson
83-84	Canada	1929	M. Newton and T. Johnson
85		1929	Minnesota
86	Bulgaria (G. G. Proytchoff) Canada	1929	
87-96**	Canada	1931	M. Newton and T. Johnson
97	Canada	1930	M. Newton and T. Johnson M. Newton and T. Johnson
98-100	South Africa	1930	
			Len Verwoerd
101	Bulgaria (G. G. Proytchoff) USA	1929	Minnesota
102* 103**	USA	1930	Minnesota
		1932	Minnesota
104-105*	USA	1931	Minnesota
106-112**	Canada	1932	M. Newton and T. Johnson
113	Canada	1930	M. Newton and T. Johnson
114-124**	Canada	1930	M. Newton and T. Johnson
125	USA	1931	Minnesota
126-128**	USA	1932	Minnesota
129-131	Turkey	1932-33	A. Scheibe
132-135	China	1933	Chih Tu
136-138**	Canada	1933	M. Newton and T. Johnson
139**	USA	1932	Minnesota
140	Mexico	1934	Minnesota

^a (See footnotes at end of table).

Table 5.—Country, year, and identifier of original collections of races 1—297 of *Puccinia graminis* var. *tritici.*—*Continued*

Races ^a	Country of Original Collection b	Year ^c	Identified by ^d
141-142	Argentina	1930	W. Rudorf
143-144	Bulgaria (D. N. Dodoff)	1931-32	Minnesota
145	Germany	1934	K. Hassebrauk
146-147**	USA	1936	Minnesota
148-158**	Canada	1936	M. Newton
159-166**	USA	1933-38	Minnesota
167*	USA	1937	Minnesota
168	USA	1937	Minnesota
169-170	Germany	1937	Hanna Becker
171	USA	1938	Minnesota
172-177**	Canada	1938	M. Newton
178	Canada (mutant of race 52)	1938	M. Newton
179	Canada	1938	M. Newton
180	Israel (G. Minz)	1937	Minnesota
181-182**	USA	1937	Minnesota
183	Canada	1938	M. Newton
184-186	Germany	1937	K. Hassebrauk
187	Portugal	1937	B. d'Oliveira
188**	USA	1939	Minnesota
189	Peru	1940	G. Garcia Rada, J. Vallega,
10)	reru	1940	and Minnesota e
190-191**	USA	1943	Minnesota
192	Canada	1941	T. Johnson
193**	Canada		
194	India	1944	T. Johnson M. K. Patel, B. N. Uppal,
194	muta	1948	and Minnesota
195	USA	1948	Minnesota
196**	USA	1948	Minnesota
197	USA	1947	
198			Minnesota
	USA	1946	Minnesota
199*	USA	1949	Minnesota
200	USA	1946	Minnesota
201**	USA	1948	Minnesota
202*	USA	1949	Minnesota
203-204	USA	1948-49	Minnesota
205	USA	1947	Minnesota
206-207*	USA	1949	Minnesota
208	USA	1949	Minnesota
209**	USA	1947	Minnesota
210	USA	1948	Minnesota
211*	USA	1948	Minnesota
212	USA	1949	Minnesota
213-230	Australia	1952	W. L. Waterhouse
231	Canada	1951	T. Johnson
232*	USA	1955	Minnesota
233	East Africa	1957-58	C. Sibilia ^f
234	Italy	1957-58	R. Basile
235	Greece	1957-58	R. Basile
236-237	Italy	1957-58	R. Basile
238-239	Italy		A. Leonori
240-244	Italy	1957-58 1957-58	R. Basile
240-244			
443-449	East Africa	1957-58	C. Sibilia

^a (See footnotes at end of table).

Table 5.—Country, year, and identifier of original collections of races 1—297 of *Puccinia graminis* var. *tritici.*—*Continued*

Races ^a	Country of Original Collection b	Year c	Identified by ^d
250-252	Italy	1957-58	R. Basile
253	Italy	1957-58	A. Leonori
254-256	Italy	1957-58	R. Basile
257	Italy	1957-58	A. Leonori
258	Italy	1957-58	G. Zitelli
259*	Italy	1957-58	R. Basile
260-266	East Africa	1957-58	C. Sibilia
267	Italy	1957-58	C. Sibilia
268	Italy	1957-58	A. Leonori
269	Italy	1957-58	R. Basile
270	Italy	1957-58	M. Rosa
271-272	Italy	1957-58	A. Leonori
273	Greece	1957-58	R. Basile
274	Italy	1957-58	G. Zitelli
275	Italy	1957-58	A. Leonori
276	Italy	1957-58	R. Basile
277	Italy	1957-58	G. Zitelli
278-279	Italy	1957-58	A. Leonori
280	Italy	1957-58	G. Zitelli
281-284	Italy	1957-58	R. Basile
285-288 g	Italy	1957-58	A. Leonori
289-291	Italy	1957-58	R. Basile
292	Italy	1957-58	G. Zitelli
293*	Italy	1957-58	R. Basile
294	Italy	1957-58	R. Basile
295	Kenya	1959	E. J. Guthrie h
296	Kenya	1960	E. J. Guthrie
297	Kenya	1961	E. J. Guthrie

^a*—From *Berberis* in field; ** from *Berberis* inoculated in greenhouse, mostly in connection with genetic studies. Asterisks apply to all numbers in an inclusive series; thus 67-72** means that races 67 to 72, inclusive, were produced on *Berberis* in the greenhouse. All other races first found in the Western Hemisphere except those designated as mutants were isolated from grains or wild grasses in the field. This is true also of most, if not all, races first found in other areas.

^b The name of the collector is given only when individuals from other countries sent material to the Minnesota Laboratory for identification. Most of the collections in the United States and Mexico were made by personnel engaged in rust epidemiology studies and in barberry eradication.

^c The numerical sequence of races is not always chronological because certain race numbers were already preempted when requests were received to assign numbers to races that antedated them in actual discovery.

^d Minnesota indicates that the identifications were made at Minnesota in the cooperative project between the U.S. Department of Agriculture and the Agricultural Experiment Station of the University of Minnesota. The following individuals participated, singly or cooperatively, in the description of one or more races: F. J. Piemeisel, M. N. Levine, R. U. Cotter, J. J. Christensen, K. Isenbeck, Lee Hines, J. M. Wallace, R. C. Cassell, W. Q. Loegering, D. M. Stewart, E. C. Stakman.

e See Garcia Rada et al. in References.

f The infection types for races 233-294 were sent to Minnesota by Prof. C. Sibilia, with the request that race numbers be assigned to those which were new. All of the data, including the identifiers of races, were furnished by Prof. Sibilia. The year 1957-58 is that in which the numbers were assigned. "East Africa" refers to the former Italian East Africa area, including Ethiopia.

g See footnote re race 285 at end of table 4; this race was finally assigned a number in 1960.

^h Dr. Guthrie authorized the inclusion of numbers 295-297 prior to his publication. On the standard differential wheat varieties these races are similar to those listed below, with the exceptions noted:

Race 295 is similar to 122 but produces type 3 on Khapli

Race 296 is similar to 11 but produces type 3 on Khapli Race 297 is similar to 41 but produces type 3+ on Vernal.

The Subdivision of Races

The extension of knowledge regarding races. Obviously all isolates identified as race 15, as an example, had 12 essentially similar characters, the infection types on the 12 standard differential varieties (Figure 6). But this general agreement in 12 characters does not imply that some of the isolates might not have differed in other characters if certain additional varieties had been inoculated. In fact, Stakman and Levine (7) stated in 1922, "It is likely that many more forms could be recognized if the proper combination of differential hosts were employed." The problem has been to find "the proper combination of differential hosts." They also stated, "The methods described can naturally be modified to meet the requirements of individual investigators, but it seems likely that preliminary indications at least can be obtained by the use of the differential hosts listed in table 1."

The possibilities implied in the above statements have become realities: the number of races that can be recognized is partly a function of the number of differential varieties which can be found to help identify them; and the 12 standard differentials have been useful in identifying races in virtually all wheat-growing countries. It is equally true, however, that the standard differentials do not reveal all of the scientifically and practically important characters of rust isolates. After having identified races by any presently feasible system, much still remains to be learned about their composition and their virulence on numerous old and new varieties of wheat and other groups of host plants. What are the biotypic components of the many isolates identified as the same race and what is the pathogenic potential of each biotype? Finality may never be attained but attempts can be made to approach it.

There are two principal reasons why any satisfactory system of classifying biotypes into races must be an extensible or open-end system. First, the components of the astronomically large populations of rust biotypes are continually changing as new biotypes, some temporary and some permanent, are being produced. Second, numerous new varieties of wheat, some of them with very complex resistance-conditioning genotypes, are continually being produced.

Knowledge regarding the composition of individual races can be extended in three principal ways: 1, by inoculating the standard differentials with a large number of isolates of each race to find out whether some isolates consistently produce different infection types within a reaction class, as in the case of 59, 59A, 59B, and 59C; 2, by testing many isolates of the same race at different temperatures to determine whether they differ in temperature requirements, as was shown by Waterhouse and Watson (13) to be true for race 34 and by Mohamed for race 139 (4); 3, by inoculating the standard differentials and a group of genetically different supplemental differentials with a large sample of isolates, as in the case of 15B, 15B-1, etc.

Terminology relating to races and their subdivisions. What is the taxonomic status of 59A, 15B, etc., and how should they be designated? Originally they were called biotypes of the respective races but this usage

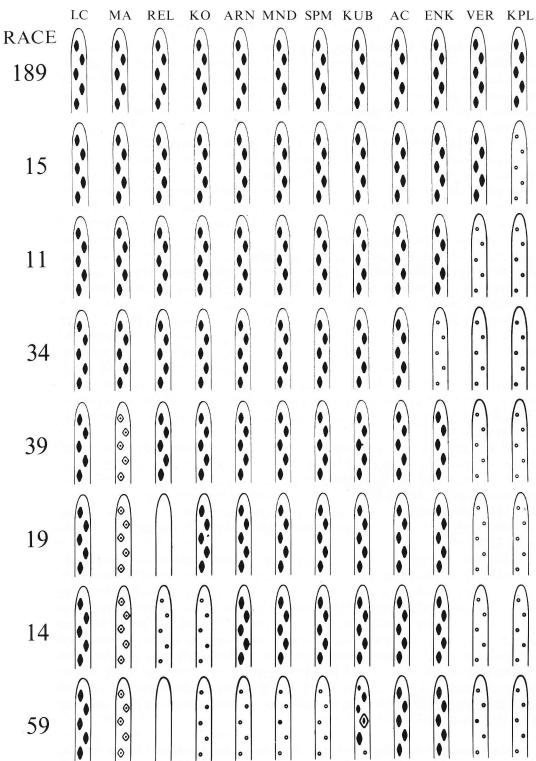


Figure 6.—Diagrammatic representation of 8 physiologic races of wheat stem rust on the standard differential varieties.

has been discontinued for reasons given on page 5. The term "subrace" has sometimes been substituted, but it has been used principally in a collective and not in a concrete sense. Thus, it has been customary to speak of "subraces of race 15," but of "race 15B." Isolates such as 59A and 59B could be considered as subraces in a true taxonomic sense if they differed from the "normal" race 59 solely in infection types within reaction classes of the 12 standard differentials. But we are dealing with an open-end system of distinctive characters and are continually discovering new characters by the use of additional criteria for their recognition. Many rust isolates that agree closely in 12 characters on the standard differentials may differ in other equally distinctive and important characters when additional differential varieties are found which reveal the differences.

Obviously, 59A, 15B, and 15B-1 are races according to the definition of race given on page 5; accordingly, the writers call them races in referring to them individually, but they also recognize the utility of the term subrace when used in a collective sense. For convenience, the term "standard race" could be applied to those races which are identified solely by means of the "standard differentials" and which produce the infection types given for that race in table 4. All "standard races," then, would have a simple numerical designation, race 1 ... race 297. For convenience also, the term "subrace" could be applied, in a collective sense, to subdivisions of standard races which have subdesignations such as 59A, 59B, 15B, 15B-1, etc. If these terms are used, however, it should be understood that they do not necessarily connote superiority and inferiority in rank or importance. Knowledge regarding the genetic relationships between the innumerable biotypes of wheat stem rust is still too meager to justify dogmatism regarding the scientific implications of certain special terms which may be used merely to facilitate communication.

Supplemental Differential Varieties

Selection and uses of supplemental differentials. A number of investigators have subdivided certain "standard races" by the use of diverse supplemental differential varieties, but it would be premature to attempt a synthesis of all of the results. Therefore some of those obtained at Minnesota are discussed as illustrative examples.

During the past decade, about 600 varieties and lines of wheat, representing a wide range of genotypes, have been tested at Minnesota as possible supplemental differentials. Only a few good differentials were found, however, and some of them are useful only within a limited range of conditions. The supplemental differentials that are presently inoculated with all isolates identified at Minnesota are listed in table 67.

Although the principal use of supplemental differentials is in subdividing certain races, some are an aid in identifying races in mixtures also, as described on page 19.

The standard races which have been subdivided are marked by asterisks in table 4, and indications are given in tables 6 and 7 of the uses

⁷ It may be possible eventually to simplify and standardize procedures by systematic use of lines of wheat having single rust-conditioning genes.

of supplemental varieties in subdividing several races which have been prevalent in North America during the past decade.

Table 6.—Supplemental differential varieties of wheat regularly used at the Cooperative Rust Laboratory at Minnesota.

Name and Origin	Uses
1. Lee , C.I. 12488 ^{-a} Hope x (Bobin ² x Gaza)	Distinguishes race 15B from race 15
2. Golden Ball, C.I. 5059	Useful in subdividing races 11, 15B, and 29
3. Selkirk , C.I. 13100 (McMurachy x Exchange) x Redman ³	Distinguishes certain isolates of 15B at 65°F, and of race 11 at 85°F.
4. Bowie , C.I. 13146 Renacimiento x Kenya C 10862	Resistant to known isolates of 15B, but susceptible to races 11E, 48A; helps in subdividing race 29
5. Kenya Farmer, C.I. 12880	Resistant to common races in North America except one isolate of race 29
6. F.K.N., C.I. 13154 Frontana x (Kenya 58 x Newthatch) II-50-17	Resistant to common races in North America except some isolates of races 11 and 29
7. Yuma, C.I. 13245 (Ld. 194 x Khapli) x Ld. 308	Useful in subdividing race 15B

^a C.I. = Cereal Investigations accession number, U. S. Department of Agriculture.

In table 7 are listed 17 varieties which have proved at least temporarily useful for the purposes indicated.

Table 7.—Supplemental test varieties of wheat which have proved useful for certain purposes at the Cooperative Rust Laboratory at Minnesota.

Variety	Races which can be subdivided
1. Triticum timopheevi Zhukov., C.I. ^a 11651	11, 15, 15B, 29
2. Kenya 117A, C.I. 12568	15B
3. Kenya 117A, Australia 1347	29
4. Magnif MG, Argentina	15B, 29, 48A
5. Magnif G, Argentina	48A
6. Conley, C.I. 13157	15B
7. North Dakota 3, C.I. 13159	11, 15B
8. North Dakota 140, C.I. 13350	15B
9. (Ill. 1 x Chinese) ² x <i>T. timopheevi</i> , C.I. 12633	15 (at 65°F. only)
0. Medea A p 9, C.I. 3255	11, 15, 15B, 29
11. Ramsey, Ĉ.I. 13246	11, 15, 15B, 29
2. Langdon, C.I. 13165	15, 15B
13. R.L. ^a 3206, C.I. 13141	11, 15, 15B, 29
14. Tremez rijo, P.I. ^a 56258-1	29
15. Towner, Č.I. 13247	15B
16. Marquillo, C.I. 6887	11 (at 65°F. only)
17. Pembina, C.I. 13332	11, 15B

 $[^]aC.I. = Cereal Investigations$ accession number, and P.I. = Plant Introduction number, U.S. Department of Agriculture; R.L. = Rust Laboratory, Canada.

Subdivision of races 15 and 29 by means of supplemental differentials. The use of supplemental differentials in subdividing standard races can be illustrated by means of results obtained with races 15 and 29.

Race 15. Three successive steps were necessary in subdividing race 15.

- 1. A Japanese isolate produced conspicuously lower infection types, within reaction classes, than other isolates and was therefore designated as 15A (2). There had long been circumstantial but not conclusive evidence also that some isolates of race 15 were exceptionally virulent on the standard differentials. A search was therefore begun for supplemental differential varieties that might give conclusive evidence of differences.
- 2. After a long search, the then new variety Lee was found to be satisfactory for separating isolates of race 15 into two groups. Those to which it was resistant continued to be designated as race 15, those to which it was susceptible were designated as 15B.
- 3. Among 317 isolates of 15B identified in the United States in 1950 there appeared to be differences in virulence on some of the susceptible standard differentials; therefore, a systematic search was made for additional differentials that might yield more conclusive evidence, and the three listed in table 8 proved useful.

Table 8.—The subdivision of race 15B by means of three supplemental differentials.

	V	arieties ^a	Race		
Isolates	SEL	GB	YU	Groups	designation
1	R b	R	R	RRR	15B-1
2	R b	R	S	R R S	15B-2
3	R b	S	R	R S R	15B-3
4	Sc	S	R	S S R	15B-4

- a. SEL=Selkirk, C.I. 13100; GB=Golden Ball, C.I. 5059; YU=Yuma, C.I. 13245.
- b. Resistant at low temperature, but susceptible at high.

c. Susceptible at all temperatures.

It is clear from table 8 that the four isolates of 15B are different. Selkirk alone distinguishes two groups, R and S, at low temperature, but it does not function as a differential at high temperature. Golden Ball and Yuma, on the other hand, function both at low and at high temperature and the two alone demonstrate that isolates 1, 2, and 3 are different, as shown by the reactions RR, RS, and SR. As concerns the identification of of these three isolates, therefore, Selkirk is superfluous; however, it differentiates between isolates 3 and 4 at low temperature and its rust reaction obviously is based on genes different from those of the other two varieties. For these reasons and because of its commercial importance, Selkirk is retained among the regular supplementals in order to find out as much as possible about its reaction to all isolates identified, which is a practical but important consideration. That race 15B can be subdivided much further is clear from studies made by Postigo (5), who proved that 14 of 17 selected isolates differed from each other on one or more of 109 varieties of wheat and barley which he inoculated.

The designations 15B, 15B-1, 15B-2, etc. represent the chronologic order in which additional information was obtained regarding race 15. When race 15 was originally described, Lee, Selkirk, and Yuma were not in existence; when Lee made possible the definite recognition of 15B, Selkirk and Yuma were not in existence. While the future variety Lee was still in increase plots, it was tested extensively for its rust resistance because of its promise as a good variety. It was inoculated with about 12,000 rust collections from the United States and Mexico, 1950 to 1960, inclusive, and was resistant to all isolates of all races except 15B. Selkirk was included also when it began to replace Lee and other spring wheat varieties. The designation 15B-1 therefore represents three chronological steps, the last two of which had to await the increase in prevalence of 15B and the development of new varieties of wheat.

Race 29. Several years ago it became important to find supplemental differentials to help distinguish between races 17 and 29 and between 38 and certain isolates of 48, because 29 and 48A were isolated from large pustules on Bowie and Travis, two new varieties of similar parentage which had been resistant in the field to the then prevalent races, including 17 and 38. As both 29 and 48A seemed to be potentially dangerous, it was desirable to determine accurately whether they were becoming more widespread and abundant (Figure 7). But it often was difficult to detect these races in mixtures with certain other races because at high temperature race 29 may look like 17 and certain isolates of race 48 (48B) may look like 38 on the standard differentials. To avoid uncertainties or considerable additional work, therefore, it became desirable to find "thermostable" supplemental differentials which would detect these races in mixtures and aid in their final identification. Bowie and Travis proved to be equally susceptible to a large sample of isolates of 29 and of 48A but resistant to 17, 38, and many other races; hence they appeared to be good but identical differentials, and Bowie was selected as a regular supplemental.

Although Bowie was chosen as a regular supplemental differential partly because of its value in helping to distinguish between races 17 and 29, it soon was found that it did not react the same to all isolates of 29. It therefore became useful in subdividing race 29 into two groups at moderate but not at high temperature. By using both Bowie and the durum C.I. 3255, however, it is possible to recognize two groups at high temperature and four at moderate temperature, as shown in table 9.

⁸ There now are indications that Lee may be susceptible to one or more isolates of another race also.

)	ear, r			Year, relative rank, and percentage of uredial isolates								
1950	'51	'52	'53	'54	'55	'56	' 57	'58	'59	'60		
п	6	8	5	6	6	4	3	2	4	3		
0.1	2.4	0.9	1.1	2.2	2.1	12.8	11.8	23.4	9.6	6.8		
0	7	9	- 11	8	9	7	7	7	7	5		
0.0	0.9	0.2	0.2	0.4	0.3	1.1	1.8	1.8	2.0	2.1		
2	ı	1	1	ı	1	2	1	3	3	2		
26.9	40.3	58.3	63.2	48,1	47.2	30.1	32.3	17.8	16.0	16.6		
3	4	5	4	3	0	0	0	0	0	0		
19.6	8.9	2.7	3.3	6.5 *	0.0	0.0	0.0	0.0	0.0	0.0		
0	0	12	10	4	2	3	4	4	2	4		
0.0	0.0	0.1	0.3	5.0	19.9	14.4	8.7	16.1	22.4	4.4		
4	3	3	3	2	5	5	5	5	6	14		
5.2	9.2	10.4	7.4	11.9	2.4	3.8	7.2	5.1	6.0	0.1		
9	8	4	9	5	4	6	6	6	5	10		
0.3	0.7	3.7	0.4	4.2	4.7	2.8	4.7	2.4	7.0	0.3		
1	2	2	2	2	3	ı	2	1	ı	L		
44.1	25.9	14.8	18.5	11.9	18.3	30.7	28.8	28.9	32.4	66.9		
	0 0.0 2 26.9 3 19.6 0 0.0 4 5.2 9 0.3	11 6 0.1 2.4 0 7 0.0 0.9 2 1 26.9 40.3 3 4 19.6 8.9 0 0 0.0 0.0 4 3 5.2 9.2 9 8 0.3 0.7 1 2	11 6 8 0.1 2.4 0.9 O 7 9 0.0 0.9 0.2 2 1 1 1 26.9 40.3 58.3 3 4 5 2.7 O 0 0 12 0.0 0.1 4 3 3 5.2 9.2 10.4 9 8 4 0.3 0.7 3.7	11 6 8 5 0.1 2.4 0.9 1.1 0 7 9 11 0.0 0.9 0.2 0.2 2 1 1 1 26.9 40.3 58.3 63.2 3 4 5 4 19.6 8.9 2.7 3.3 0 0 12 10 0.0 0.1 0.3 4 3 3 3 5.2 9.2 10.4 7.4 9 8 4 9 0.3 0.7 3.7 0.4 1 2 2 2	11 6 8 5 6 0.1 2.4 0.9 1.1 2.2 0 7 9 11 8 0.0 0.9 0.2 0.2 0.4 2 1 1 1 1 3 4 5 4 3 19.6 8.9 2.7 3.3 6.5 0 0 12 10 4 0.0 0.0 0.1 0.3 5.0 4 3 3 3 2 5.2 9.2 10.4 7.4 11.9 9 8 4 9 5 0.3 0.7 3.7 0.4 4.2 1 2 2 2 2	11 6 8 5 6 6 0.1 2.4 0.9 1.1 2.2 2.1 0 7 9 11 8 9 0.0 0.9 0.2 0.2 0.4 0.3 2 1 1 1 1 1 47.2 3 4 5 4 3 0 0.0 0.0 0.0 0.0 0.0 0.0 0.0 0.0 0.0 0.0 0.1 0.3 5.0 19.9 4 3 3 3 2 5 5 5 0.0 19.9 4 3 3 3 2 5 5 0.0 19.9 0.0 0.0 0.0 0.0 10.4 7.4 11.9 2.4 0.4 0.0	11 6 8 5 6 6 4 0.1 2.4 0.9 1.1 2.2 2.1 12.8 0 7 9 11 8 9 7 0.0 0.9 0.2 0.2 0.4 0.3 1.1 2 1 1 1 1 1 2 47.2 30.1 3 4 5 4 3 0 0 0 0 0 0.0 0	11 6 8 5 6 6 4 3 0.1 2.4 0.9 1.1 2.2 2.1 12.8 11.8 0 7 9 11 8 9 7 7 0.0 0.9 0.2 0.2 0.4 0.3 1.1 1.8 2 1 1 1 1 1 2 1 30.1 32.3 3 4 5 4 3 0	11 6 8 5 6 6 4 3 2 0.1 2.4 0.9 1.1 2.2 2.1 12.8 11.8 23.4 0 7 9 11 8 9 7 7 7 0.0 0.9 0.2 0.2 0.4 0.3 1.1 1.8 1.8 2 1 1 1 1 1 2 1 3 32.3 17.8 3 4 5 4 3 0 </td <td>11 6 8 5 6 6 4 3 2 4 0.1 2.4 0.9 1.1 2.2 2.1 12.8 11.8 23.4 9.6 0 7 9 11 8 9 7 7 7 7 0.0 0.9 0.2 0.2 0.4 0.3 1.1 1.8 1.8 2.0 2 1 1 1 1 1 2 1 3 3 3 3 4 5 4 3 0</td>	11 6 8 5 6 6 4 3 2 4 0.1 2.4 0.9 1.1 2.2 2.1 12.8 11.8 23.4 9.6 0 7 9 11 8 9 7 7 7 7 0.0 0.9 0.2 0.2 0.4 0.3 1.1 1.8 1.8 2.0 2 1 1 1 1 1 2 1 3 3 3 3 4 5 4 3 0		

¥ 17-29 Group

Figure 7.—Relative prevalence of 8 races of wheat stem rust in the United States, 1950-1960, inclusive.

Table 9.—The subdivision of race 29 by means of two supplemental differential varieties of wheat ^a

		V	ariety, te	mperature i react	n degree ion clas		eit, and		Race
Isolates		Bowie		(C.I. 325	5	Grou	ıps	designation
	65°	75°	85°	65°	75°	85°	65°-75°	85°	
A	R	R	S	R	R	R	RR	SR	29 A
В	R	R	S	S	S	S	RS	SS	29 B
C	S	S	S	R	R	R	SR	SR	29 C
D	S	S	S	S	S	S	SS	SS	29 D
Groups	RS	RS	S	RS	RS	RS	4	2	

^a These data were furnished by James D. Miller of the Cooperative Rust Laboratory at Minnesota, and have been published in a preliminary paper (3).

From table 9 it is evident that the four isolates, A, B, C, D, of race 29 are different, but all of the differences are apparent only at temperatures of 75°F. or lower, as Bowie is susceptible to all isolates at 85° and there appear to be only two groups, SR and SS. At 65-75°, however, it is clear that there are four: RR, RS, SR, SS. In a case like this, determinations should be made, if possible, at about 70° or lower, as the change from R to S on Bowie is likely to begin at about 75° and the infection type at this temperature may simulate type X, thus causing uncertainty in the case of unknown isolates. It would be desirable to use only differential varieties whose reactions are thermostable, but, until they can be found, determinations must be made at temperatures that reveal the differences between isolates.

The data in table 9 on the reactions of Bowie to the four isolates of race 29 show how important it is to determine the range of variability of thermolabile race-variety combinations. The implication is obvious and has been emphasized several times; caution is essential in drawing conclusions about many race-variety combinations unless tests can be made at appropriate temperatures.

Method of designating subdivisions of races. As concerns the designation of subdivisions of races identified by use of supplemental differentials or otherwise, the practice at the Minnesota Cooperative Rust Laboratory is to designate the first recognized ones with a capital letter, such as 59A and 15B. If these can be further subdivided, the designations are 15B-1, 15B-2, etc. Uniformity in designation is, of course, desirable. As an example, isolates of standard race 15 that have the additional ability to cause heavy infection on a supplemental differential, Lee, have been designated as 15B, and it would cause confusion if 15B were used in another

⁹ This is the practice also at the Canada Department of Agriculture Research Laboratory, Winnipeg, and is in conformity with an informal agreement described in a memorandum issued by the Cooperative Rust Laboratory at Minnesota on April 10, 1957. The reason for using both letters and subnumbers, such as 15B-1, etc., is that the use of letters had become established before it was known that further subdivision was possible.

sense. The 15B-1, 15B-2, etc., as used in this paper, were designations based on the reactions of Selkirk, Golden Ball, and Yuma; the 29A, 29B, etc., were designations based on the reactions of Bowie and C.I. 3255. But investigators in other countries might discover subraces in the course of tests on varieties of greater importance to them, and they might use the same designations for their subraces. The question then arises as to whether the subraces designated as 15B-1 in different countries are the same or different. It would be desirable to find out eventually and to prepare tables of equivalents, if possible.

It is suggested that it would be desirable to use a uniform system of designation, and, when the basis of determination is peculiar to a given country, to so indicate. Thus, the designations might be 15B-1 (U.S.A.), 15B-1 (Kenya), etc. As the basis for determination would naturally be published also, this procedure could facilitate the preparation of an "International Table of Equivalents" or "Register of Races and Subraces."

Conclusion

The determination of physiologic races is detailed taxonomy, with two objectives: (1) to learn as much as possible about the innumerable biotypes and to group them in a useful way, and (2) the practical objective of helping to understand and control plant diseases. A proximate classification of races of *Puccinia graminis* var. *tritici* is relatively simple. The problem becomes much more complex as attempts are made to approach closer to the recognition and identification of individual biotypes. Attempts should be intensified to understand the gene-for-gene relationships in the rust pathogen and in wheat, but, to attain the practical objective of learning the effects of physiologic races on important varieties, not only the individual genes present but their behavior in a given genotype is important. Obviously, therefore, varieties themselves must be tested, unless some way is devised to predict the performance of races with many genes that condition virulence on wheat varieties with many genes that condition rust reaction.

In the present state of knowledge it seems expedient to maintain a system based on the standard differentials, which have been widely used for about 40 years, but also to leave the way open for flexibility in the finer analysis of rust populations, at least until facilities may be provided for an adequate world-wide study of the wheat stem-rust pathogen.

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